CENOZOIC HISTORY OF SOME WESTERN AMERICAN PINES[1]

DANIEL I. AXELROD[2]

ABSTRACT

Since *Pinus* occurs in the Early Cretaceous (ca. 125–130 Ma), it probably had emerged from a *Pityostrobus* complex by the Late Jurassic (ca. 140–135 Ma). Initial adaptation to seasonal climate and drier sites may account for rapid evolution on several occasions. This presumably was enhanced by symbiotic association with ectotrophic mycorrhizae that gave pines an adaptive advantage in new, spreading, more stressful environments throughout its history. *Pinus* probably underwent major splitting into early subsections in the Late Cretaceous-Early Tertiary as Laramide tectonism created new environments (dry slopes, rain shadows). In the later Eocene-Oligocene, new opportunities for speciation resulted from increased tectonism, volcanism, and the spread of regional dry climate. New drier sites appeared in the Late Oligocene (28–27 Ma) as erosion increased in response to lowered base level as sea level decreased and as Drakes Passage opened and cold water was shunted northward. Further speciation no doubt occurred as seasonally dry climates spread in response to developing ice sheets (East Antarctic, 13 Ma; West Antarctic, 7–6 Ma; Arctic, 4–3 Ma). Continued volcanism, tectonism, and markedly fluctuating climate at the close of the Cenozoic fostered further speciation, especially in Mexico where pines show much intergradation owing to rampant hybridization in the recent past. Species of three subsections (*Cembrae, Strobi, Sylvestres*) in North America are represented by taxa in Eurasia. They reflect the early spread of ancestral taxa into both land areas via connections across the mid-to-north Atlantic and Beringian areas. Neogene records in Europe of taxa allied to east American pines (*Australes*) may be valid but need reevaluation. The fossil record suggests that six of the eight subsections indigenous to North America (*Balfourianae, Cembroides, Leiophyllae, Oocarpae, Ponderosae, Sabinianae*) probably originated over the Cordilleran region that extends southward into Mexico. Subsect. *Australes* may be largely southeastern and the *Contortae* evidently spread northward (*P. contorta, P. banksiana*) and into mountains as colder environments appeared there. Movement along the San Andreas rift system probably transported taxa northward from western Mexico, as indicated by species of *Oocarpae, Leiophyllae,* and *Strobi* in Tertiary rocks of coastal California. As more extreme climates spread in the late Cenozoic, the richer Tertiary forests and woodlands lost taxa, and the survivors retreated to moister areas. Pines now increased numerically as competition was reduced and more space appeared in the impoverished, surviving vegetation zones. In addition, spreading new regional environments, notably drier lowlands (for piñons), drier upland slopes (for *P. ponderosa, P. scopulorum, P. jeffreyi, P. flexilis*), colder, wetter basins (for *P. banksiana, P. contorta*), and cold uplands (for *P. albicaulis, P. aristata, P. contorta, P. monticola*), now became available as more continental climates spread. Pines in these more extreme environments, where they are also associated with ectotrophic mycorrhizae, may form regionally extensive, pure stands. These are not recorded in presently-known Tertiary floras in which pines were members of rich, mixed conifer, conifer hardwood, and sclerophyllous woodland vegetation. During the past few centuries, some pines greatly increased in number as man upset ecosystems by fire, logging, and clearing.

PART 1. HISTORY

Fossil records of Pinaceae are rare in most Cretaceous to early Paleogene rocks. This is because they lived chiefly in sites well removed from the lowland broadleaved forests adapted to warm temperate to tropical, essentially aseasonal, climates of ample rainfall. These conditions were the result of low, widely-flooded continents, the lack of high mountain chains and plateaus,

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[1] Many of the fossil pines on which this paper is based were secured by me during the collection of Tertiary floras over the past 50 years. This was made possible by grants from the Carnegie Institution of Washington (1935–1952), the National Science Foundation (1954–), and, intermittently, by the Committees on Research, University of California, Los Angeles and Davis campuses. Acknowledgment is due W. B. Critchfield for permission to compare the remains of fossil pines with the large, excellent collection of modern pines at the Institute of Forest Genetics, Placerville, California. Thanks are also extended to F. M. Hueber, Smithsonian Institution and to J. W. Hall, University of Minnesota, for the loan of critical pine fossils described in earlier reports. In addition, Ruth A. Kirkby, Director of the Jurupa Mountains Cultural Center, Riverside, California, generously granted me permission to study and photograph specimens of *Pinus lindgrenii* Knowlton that she collected in the type area near Bruneau, southern Idaho. The photographs of many of the fossils were taken by Howard Schorn, Dept. Paleontology, University of California, Berkeley. W. B. Critchfield, J. R. Haller, C. Millar, C. N. Miller, Jr., and P. H. Raven reviewed the manuscript and have offered a number of valuable suggestions that have improved it.

[2] Department of Botany, University of California, Davis, California 95616.

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TABLE 1. Subdivisions of genus *Pinus* (after Little & Critchfield, 1969).

		Number of Species	
		*North America	Eurasia
Pinus			
Subgenus 1. DUCAMPOPINUS			
Sect. 1. *Ducamptopinus*		–	1
Subsect. 1. *Krempfianae*			
Subgenus STROBUS			
Sect. 2. *Strobus*			
Subsect. 2. *Cembrae*		1	4
P. albicaulis Engelm.			
3. *Strobi*		6	8
P. ayacahuite Ehrenb.	*P. monticola* Dougl.		
flexilis James	*strobiformis* Engelm.		
lambertiana Dougl.	*strobus* L.		
Sect. 3. *Parrya*			
Subsect. 4. *Cembroides*		8	–
P. cembroides Zucc.	*P. monophylla* Torr. & Fremont		
culminicola Andres. & Beaman	*nelsonii* Shaw		
edulis Engelm.	*pinceana* Gord.		
maximartinezii Rzedow.	*quadrifolia* Parl.		
5. *Gerardianae*		–	2
6. *Balfourianae*		3	–
P. aristata Engelm.			
balfouriana Grev. & Balf.			
longaeva Bailey			
Subgenus PINUS			
Sect. *Ternatae*			
Subsect. 7. *Leiophyllae*		2	–
P. leiophylla Scheide & Deppe			
lumholtzii Robins. & Fern.			
8. *Canarienses*		–	2
9. *Pineae*		–	1
Sect. 5. *Pinus*			
Subsect. 10. *Sylvestres*		2	17
P. resinosa Ait.			
tropicalis Morelet			
11. *Australes*		11	–
P. caribaea Morelet	*P. occidentalis* Sw.		
cubensis Griseb.	*palustris* Mill.		
echinata Mill.	*pungens* Lamb.		
elliottii Engelm.	*rigida* Mill.		
glabra Walt.	*serotina* Michx.		
	taeda L.		
12. *Ponderosae*		14	–
P. arizonica C. E. Blanco	*P. michoacana* Martinez		
douglasiana Martinez	*montezumae* Lamb.		
durangensis Martinez	*ponderosa* Laws.		
engelmannii Carr.	*pseudostrobus* Lindl.		
hartwegii Lindl.	*teocote* Scheide & Deppe		
jeffreyi Grev. & Balf.	*washoensis* Mason & Stockwell		
lawsonii Roezl			

TABLE 1. Continued.

		Number of Species	
		*North America	Eurasia
13. *Sabinianae*		3	–
P. coulteri D. Don			
sabiniana Dougl.			
torreyana Parry			
14. *Contortae*		4	–
P. banksiana Lamb.	*P. contorta* Dougl.		
clausa (Chapm.) Vasey	*virginiana* Mill.		
15. *Oocarpae*		8	–
P. attenuata Lemm.	*P. patula* Schiede & Deppe		
greggii Engelm.	*pringlei* Shaw		
muricata D. Don	*radiata* D. Don		
oocarpa Schiede	*remorata* Mason		
	Totals	62	35

* Names of American species only are listed here; from Little and Critchfield, 1969, plus *P. remorata* in *Oocarpae.*

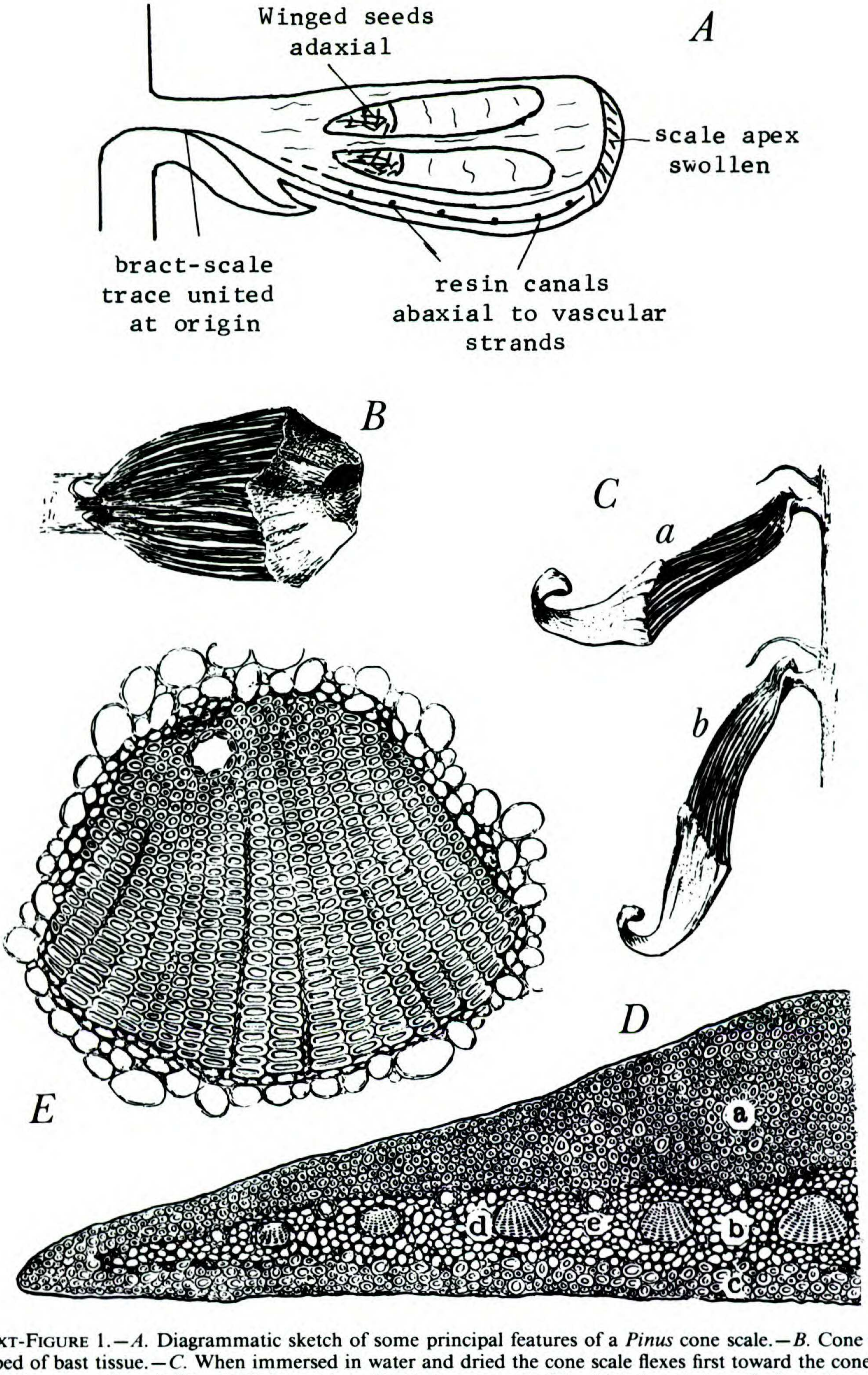
and the absence of polar ice caps. By contrast, Pinaceae, and *Pinus* in particular, adapted early to seasonal climates. This is apparent from the records of relatively abundant Pinaceae (*Abies, Picea, Pinus, Pseudotsuga, Tsuga*) in the few montane floras that are known. Examples include the Princeton flora, British Columbia (Arnold, 1955; Miller, 1973; Stockey, 1984), the Copper Basin (Axelrod, 1966a) and Bull Run floras (in Axelrod, 1968, MS), northeastern Nevada, and the Florissant (MacGinitie, 1953) and Creede (Knowlton, 1923; Axelrod, unpubl. data) of Colorado. The Paleogene floras of arctic and subarctic regions also have remains of Pinaceae, including *Pinus* (Heer, 1868–1883). In view of these circumstances, we know relatively little of the initial history of *Pinus.* The earliest records of presumed pine-like taxa (see Miller, 1977a) include needles and cones that are not readily referred to modern groups of pine. Most of the Cretaceous cones whose internal structure has been examined represent *Pityostrobus,* an ancestral plexus from which *Pinus* had emerged by the Early Cretaceous (ca. 130–125 Ma) (Alvin, 1960). More numerous fossil pines come into the record in the Eocene, and they increased in abundance down to the present.

Pinus now includes 95 species that have been grouped into three subgenera, *Ducampopinus, Strobus,* and *Pinus* (Table 1). Of the 15 subsections, only three occur in both North America and Eurasia, notably *Cembrae* and *Strobi* of Subgenus *Strobus,* and *Sylvestres* of Subgenus *Pinus.* The 11 subsections in North America (Subgenus *Strobus* with four, Subgenus *Pinus* with seven) include about 62 taxa, or nearly two-thirds of all pine species. These are concentrated in Mexico with 28 species, and in California with 20. Larger regions elsewhere have fewer species, notably eastern Asia (14 spp.), southern Asia (seven spp.), and southern Europe (eight spp.).

To infer the modes and times of origin of these groups, and the manner in which present distributions may have developed, we turn to the fossil record. It is incomplete, yet it does contain the only historical facts (fossils) available for analysis. Interpretations of these remains may vary, because investigators have concentrated on different modes of analysis. Some have studied the internal structure of cones and needles where these have been available, though they are indeed few in number. Most remains of Tertiary pines occur as imprints in fine tuffaceous shale and sandstone preserved in lake beds and floodplain deposits of Cenozoic age. Both lines of evidence are reviewed here so as to arrive at a provisional, and hopefully better, understanding of pine history in North America.

EARLY ORIGIN AND EVOLUTION

Some fossil ovulate cones outwardly similar to those of *Pinus* have been designated *Pityostrobus.* They differ internally from *Pinus* cones in several ways (Miller, 1976). All of the presently known 20-odd Cretaceous cones that have



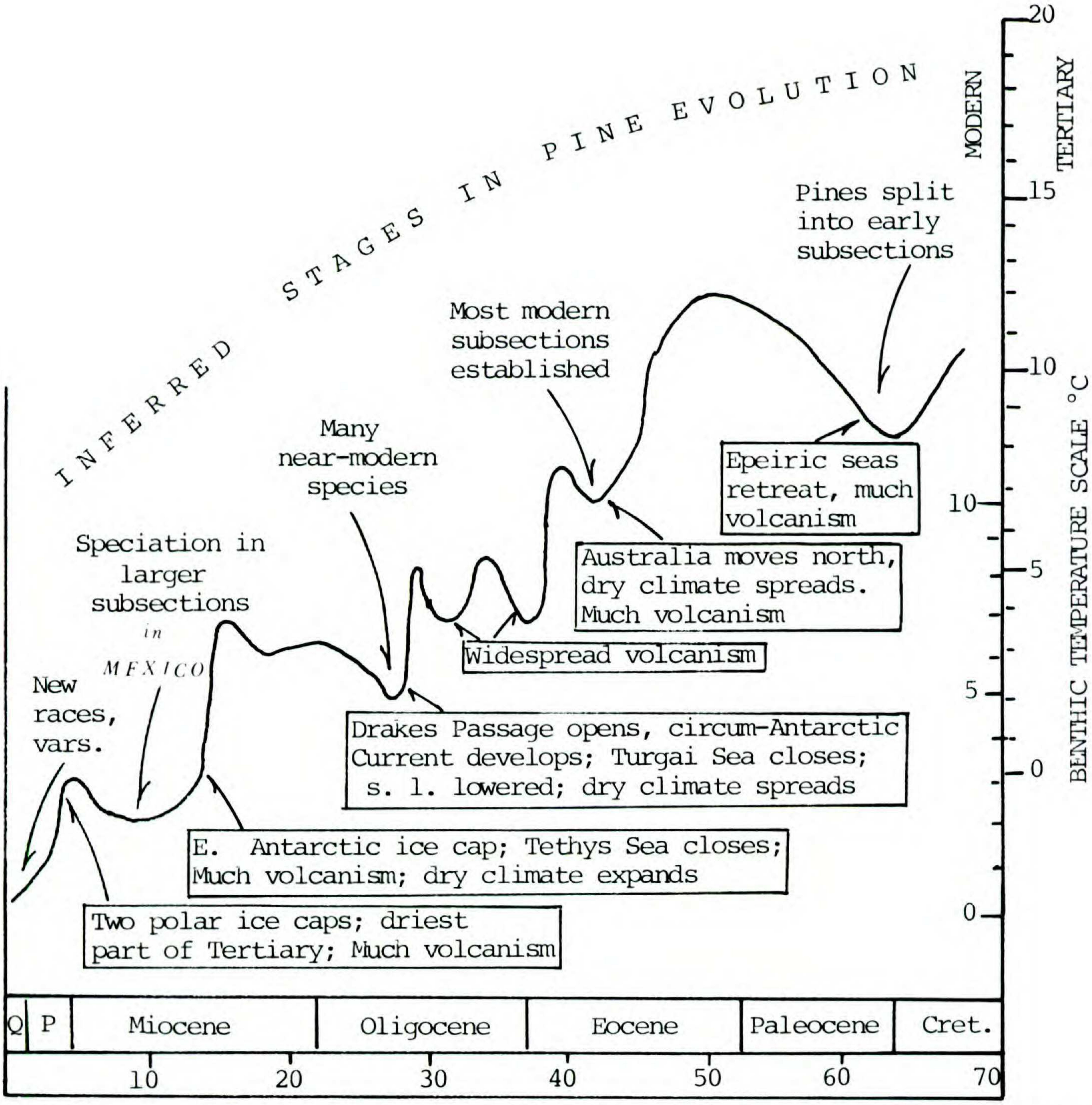
TEXT-FIGURE 1.—*A.* Diagrammatic sketch of some principal features of a *Pinus* cone scale.—*B.* Cone scale stripped of bast tissue.—*C.* When immersed in water and dried the cone scale flexes first toward the cone axis (*a*) and then away from it (*b*).—*D.* Cross section of half of a cone scale. The thick dorsal plate of sclerenchymatous cells (*a*) and a thinner ventral plate (*c*). Soft brown tissue (*b*) encloses vascular strands (*d*). Resin ducts (*e*).—*E.* Vascular strand enlarged. (Figs. B–E from G. R. Shaw, with permission of Arnold Arboretum.)

been examined structurally may have none or one or two of the internal features of *Pinus* (Miller, 1976, table 2). These include an inflated scale apex, bract-scale trace united at origin, resin canals abaxial to vascular tissue in the scale base, and scale strands curved on abaxial side (Text-Fig. 1). The first three features are present only in *Pinus* cones. The fourth is in all *Pinus* species and is rare and atypical in cones of other pinaceous genera (Miller, 1976, 1977a). The reviews by Miller (1976, 1977a) make it apparent that *Pityostrobus* is central to pine evolution. Inasmuch as *Pinus belgica* Alvin (1960) is in the Early Cretaceous (ca. 120–125 Ma), and represents Subgenus *Pinus* (Miller, 1977a) on the basis of its internal structure, it demonstrates the antiquity of the subgenus. In his reviews of Mesozoic conifers, Miller (1976, 1977a) noted that leaves with internal structure of two vascular strands also indicate affinity with Subgenus *Pinus*. Cretaceous cones reportedly allied to Subgenus *Strobus* may represent *Pityostrobus*, but these have not been examined internally. Certainly by the Eocene, species of the *Strobus* alliance were well established (see below).

Most described Cretaceous species of *Pityostrobus* and *Pinus* now occur at middle-high latitudes, as in Belgium, England, Massachusetts, Virginia, and New Jersey. However, the evidence of plate tectonics (Smith et al., 1981) shows that these areas were near Lat. 30–35°N in the Jurassic-Early Cretaceous. Climates were seasonally dry as shown by saline deposits and red beds (Hallum, 1984). By the Paleocene, pines were present at higher latitudes (70–80°N), although a cone of *Pityostrobus* (*P. lynnii* Berry) is recorded from the Paleocene of Virginia (Miller, 1977b). Available evidence suggests that the *Pityostrobus* plexus originated over low-middle latitudes and that it probably gave rise to *Pinus* by the Late Jurassic. *Pinus* was then adapted to seasonal climate in middle latitudes, as well as in the montane subtropics, and had spread into seasonal climates of middle and higher latitudes by the close of the Cretaceous (ca. 65 Ma).

Mirov (1967) inferred from both their morphology and physiology that modern pines originated not in uniformly hot, humid climates, but in those with alternating seasons, either wet and dry, or warm and cold, or a combination of both. Most living pines occur where there is ample sunshine, where the soil is porous, generally poor in nutrients, and well drained. They are xerophytes, for they withstand considerable drought and most show little tolerance of shade. Most pines inhabit exposed slopes away from rich, mesic valley forests. They now occupy diverse climates, ranging through temperate forested regions up to timberline, to semi-arid plateaus and desert-border environments, and to the tropics where there is a prolonged dry season, as in Cuba, Haiti, Nicaragua, Taiwan, Luzon, and Laos.

Their early adaptation to seasonal conditions no doubt favored their ability to seize new environmental opportunities later in their history. Diversity of terrain developed during the Laramide orogeny in the Late Cretaceous-Early Tertiary. This may well have been a time of splitting into forerunners of the principal subsections, the species of which are now extinct. By the Middle Eocene (ca. 45 Ma), there was a major shift to spreading dry climate in southwestern North America (Text-Fig. 2). This created conditions favorable for speciation in *Pinus*. In addition, active volcanism, extending from Wyoming-Montana southward through the Sierra Madre Occidental, Mexico, provided new, drier sites for the origination of taxa in spreading seasonal climate. By the Late Eocene (35 Ma), dry climate covered much of the western interior and far south into Mexico, and more seasonal conditions were developing (Axelrod & Raven, 1985). Continuing volcanism into the Oligocene (ca. 26.5 Ma) favored further diversification as indicated by the occurrence of numerous near-modern species. At this time, evolution was enhanced by the spread of drier conditions. As Drakes Passage opened, colder water that developed around Antarctica subsided and spread northward to rise in the low–middle latitudes, bringing drier climates there. In addition, as sea level was rapidly lowered in the Late Oligocene (ca. 27–26 Ma) (Vail et al., 1977; Vail & Hardenbol, 1979), more land area was exposed and continentality increased. With lowered base level, landscapes were rejuvenated by erosion, creating new slopes for occupation by pines and other plants adapted to drier, well-drained sites. Environments would be affected in both coastal and interior areas. In the coastal strip, the spread of drier sites may account for speciation of some *Australes* in the southeastern states. In the interior, new species of *Ponderosae, Oocarpae,* and *Cembroides* may have arisen, especially since tectonism and volcanism were active there. Middle Tertiary environments appear to have been similar to those now in the uplands of Mexico where active speciation is occurring today, and has in the recent



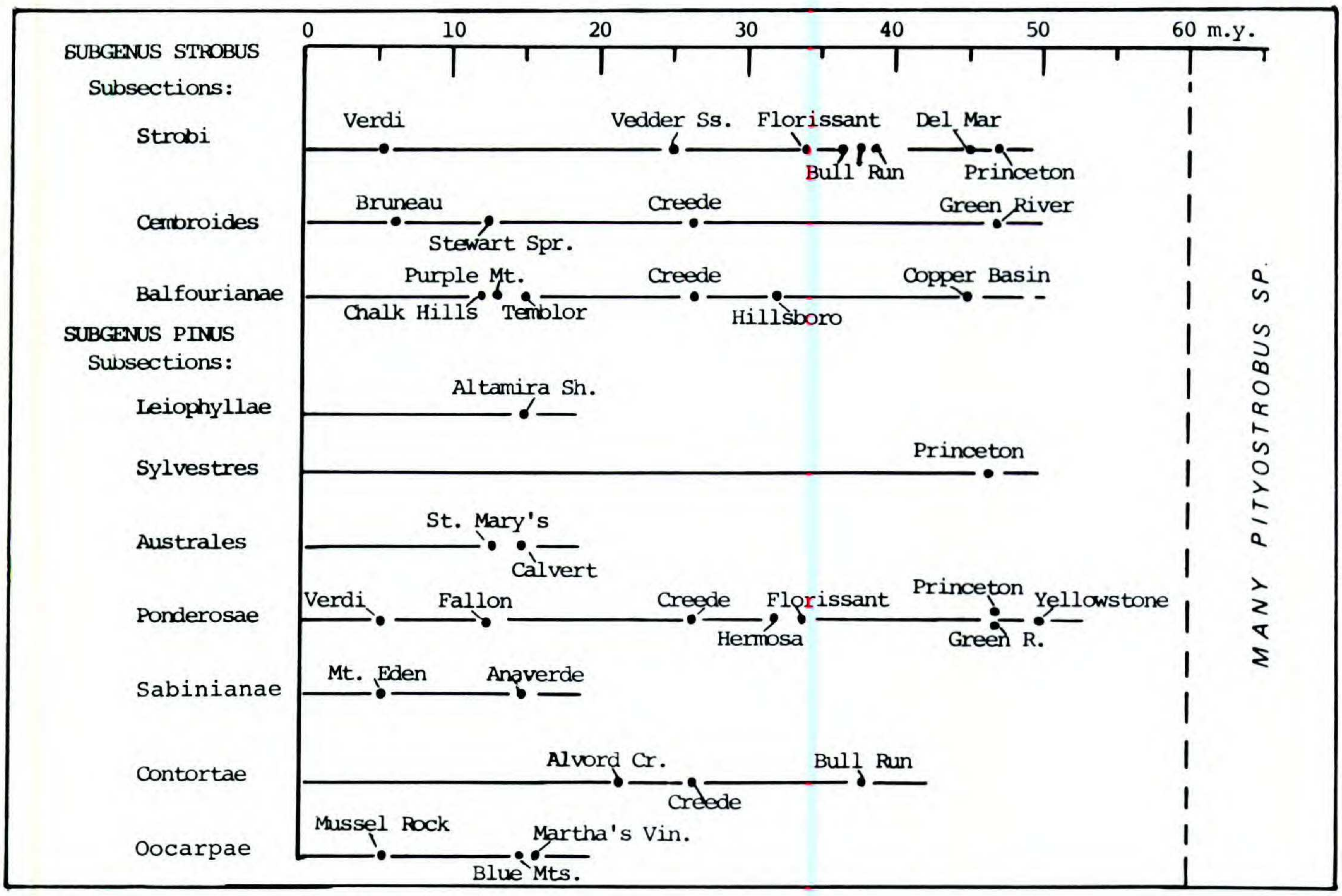
TEXT-FIGURE 2. Inferred correlation of environmental changes with pine evolution. Temperature curve from Savin, 1977. Early adaptation to drier, poorer sites aided by their association with ectotrophic mycorrhizae enabled pines to diversify as these conditions spread during the Tertiary.

past (Mirov, 1967: 341–345). Speciation was further enhanced in the late Cenozoic by fluctuating climate, the building of major volcanos, uplift of plateaus and bordering mountains, and the spread of drier and colder climates to which the taxa were adapted—all conditions favoring major, rapid changes in populations (Stebbins, 1974).

The ages of the older Tertiary species that may be assigned to American subsections of Subgenera *Strobus* and *Pinus* are indicated in Text-Figure 3. It is evident that their origins lie in earlier times, as the preceding inferences regarding environmental changes suggest. This may also be inferred from the distributions and ecological adaptations of taxa of *Pinus* subsections.

1. In Subgenus *Strobus,* the four species of Subsect. *Cembrae* have widely discontinuous distribution across Holarctica. *Pinus albicaulis* is in the high mountains of the western United States and adjacent Canada, *P. cembra* occupies the mountains of southern Europe, and *P. pumila* and *P. sibirica* range widely across central and eastern Siberia (Text-Fig. 4).

2. In Subgenus *Strobus* (Text-Fig. 5), Subsect.



TEXT-FIGURE 3. Ages of fossil pines of American subsections of Genus *Pinus*.

Strobi has 14 species widely scattered in forests across middle to low-middle latitudes in North America from southern Canada to El Salvador and Guatemala, and in Eurasia from Japan to the Himalayas and Vietnam, and to Albania in southern Europe.

3. In Sect. *Parrya* (Text-Fig. 6), Subsect. *Cembroides* (8 spp.) occupies the drier parts of western North America, whereas Subsect. *Balfourianae* (3 spp.) is in moister and/or colder montane regions. Taxa of these two subsections are very different morphologically and ecologically and also differ greatly from species of Subsect. *Gerardianae* (2 spp.) now in the Pamir region (*P. gerardiana*) and north-central China (*P. bungeana*).

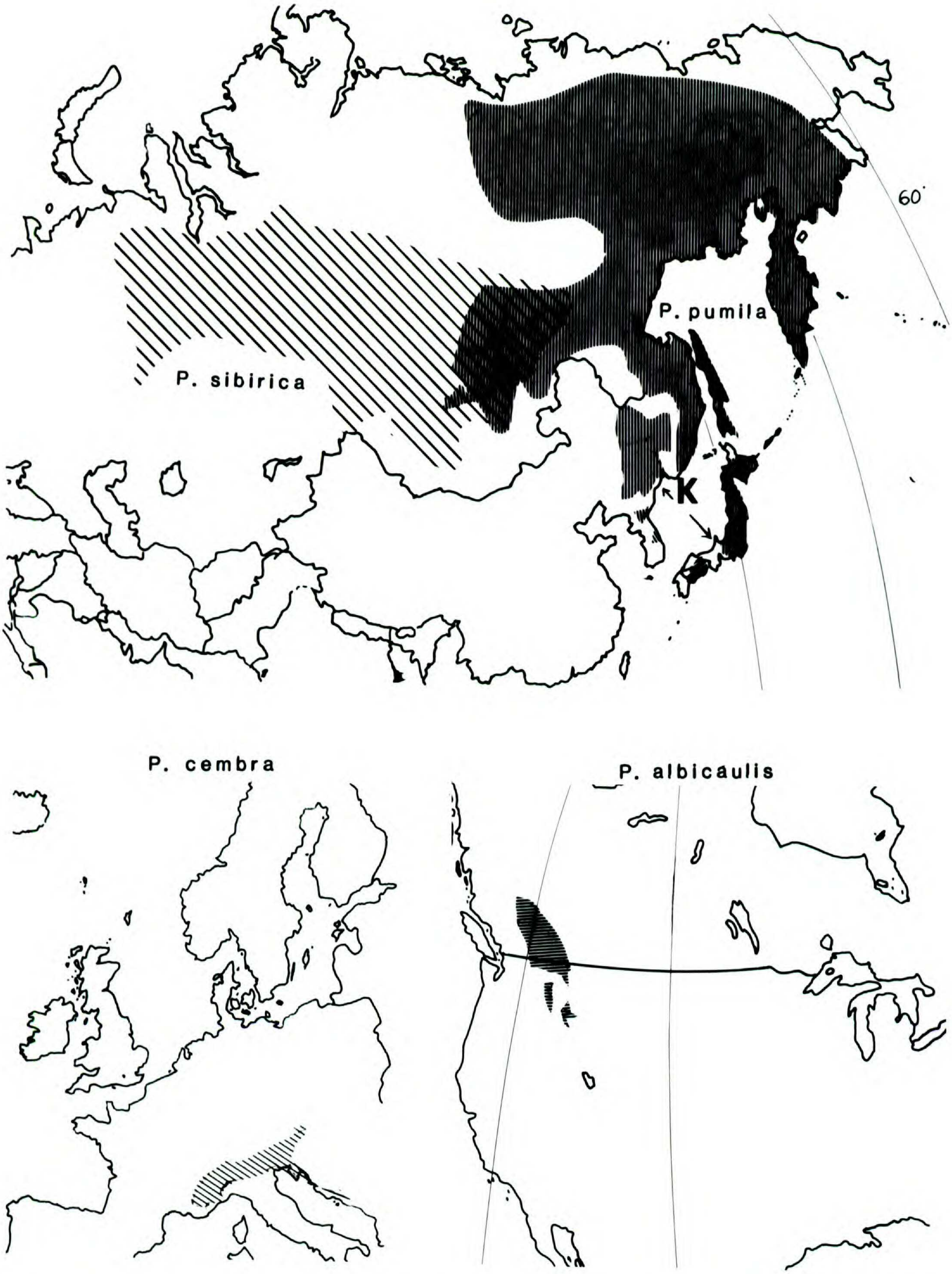
4. Sect. *Ternatae* includes Subsect. *Leiophyllae* (2 spp.) in Mexico and southern Arizona, Subsect. *Canarienses* (2 spp.) of the Canary Islands (*P. canariensis*) and the Himalayas (*P. roxburghii*), and Subsect. *Pineae* (1 sp.) of southern Europe-Asia Minor (*P. pinea*) (Text-Fig. 7).

5. In Sect. *Pinus*, Subsect. *Sylvestres* with 19 taxa is chiefly Eurasian. The two American species are adapted to dissimilar climates, cold temperate for *P. resinosa*, tropical for *P. tropicalis*. A similar disjunction in adaptation is apparent for the 17 Eurasian taxa (Text-Fig. 8), the temperate species of which are presumably derived.

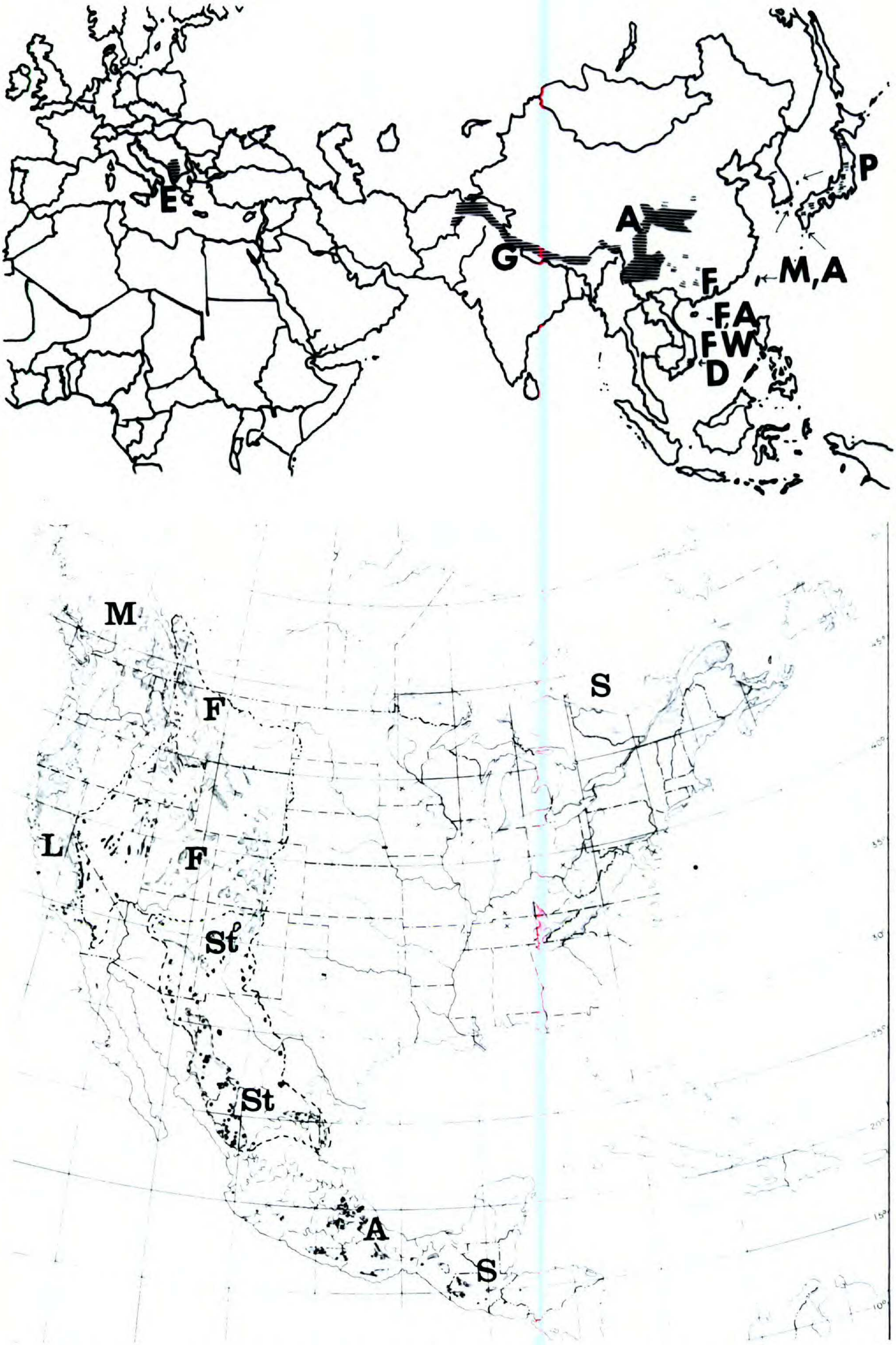
The distinctness of these subsections (see Little & Critchfield, 1969), their disparate distributions (see Critchfield & Little, 1966), and their different climatic adaptations, all imply considerable age. This inference is supported by the fossil record, for most of these alliances occur in the Oligocene, and some are represented by taxa in the Eocene (Text-Fig. 3). The evidence again suggests that evolution of the modern subsections was well under way in the Eocene and probably had commenced earlier for some, relations consistent with comparative immunological and amino acid sequence studies of proteins (Prager et al., 1976).

TERTIARY HISTORY OF AMERICAN SUBSECTIONS

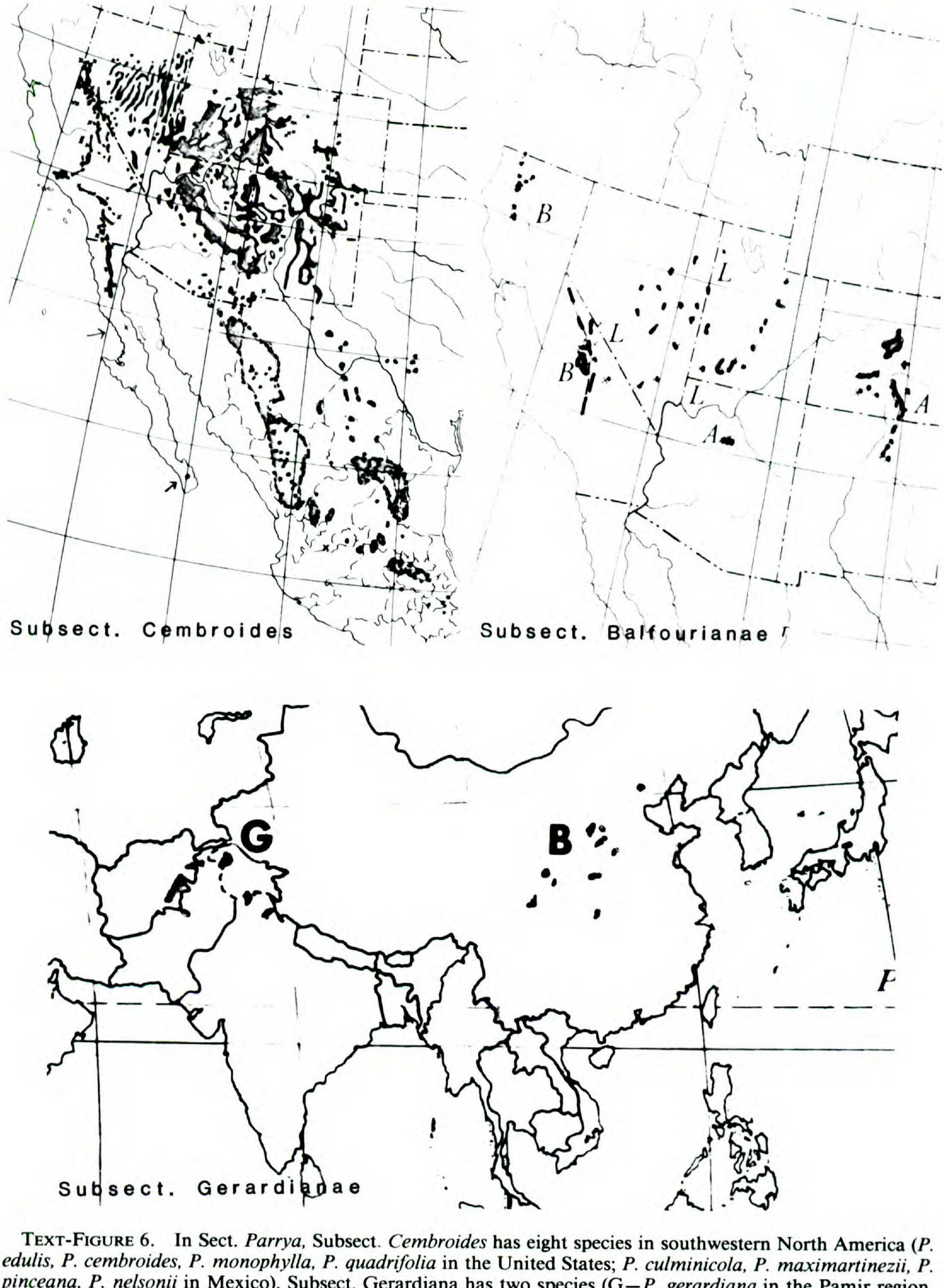
The records of Tertiary pines indicate that species of three subsections (e.g., *Cembrae, Sylvestres, Strobi*) now common to North America and Eurasia probably were established by the Paleogene. By contrast, eight subsections now restricted to North America, and the four to Eur-



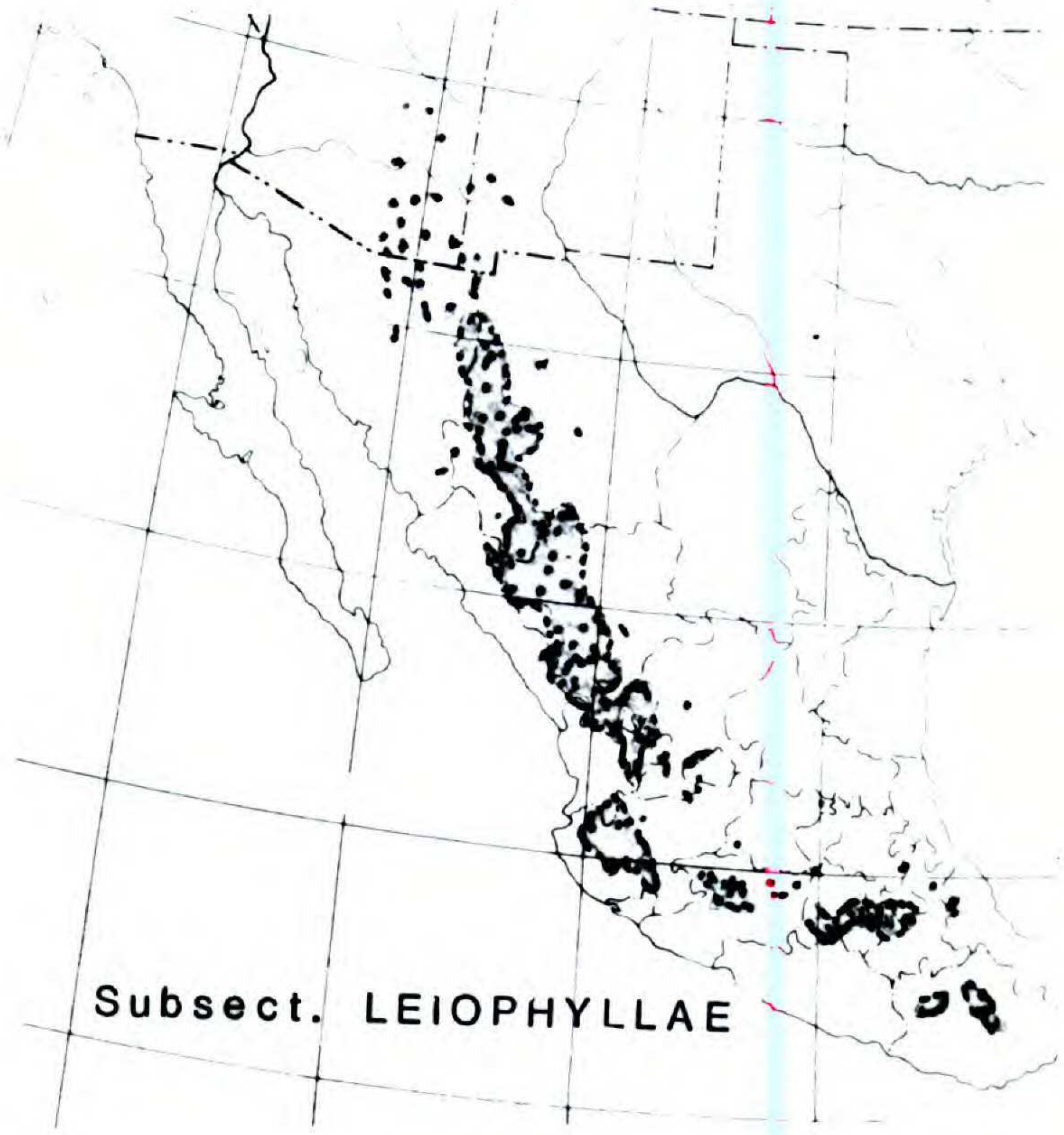
TEXT-FIGURE 4. In Sect. *Strobus,* Subsect. *Cembrae* has a discontinuous distribution across Holarctica (K = *P. koraiensis*). The Eurasian taxa have finely serulate needles, the American is entire. Was *Cembrae* represented in northeastern North America during the later Tertiary?

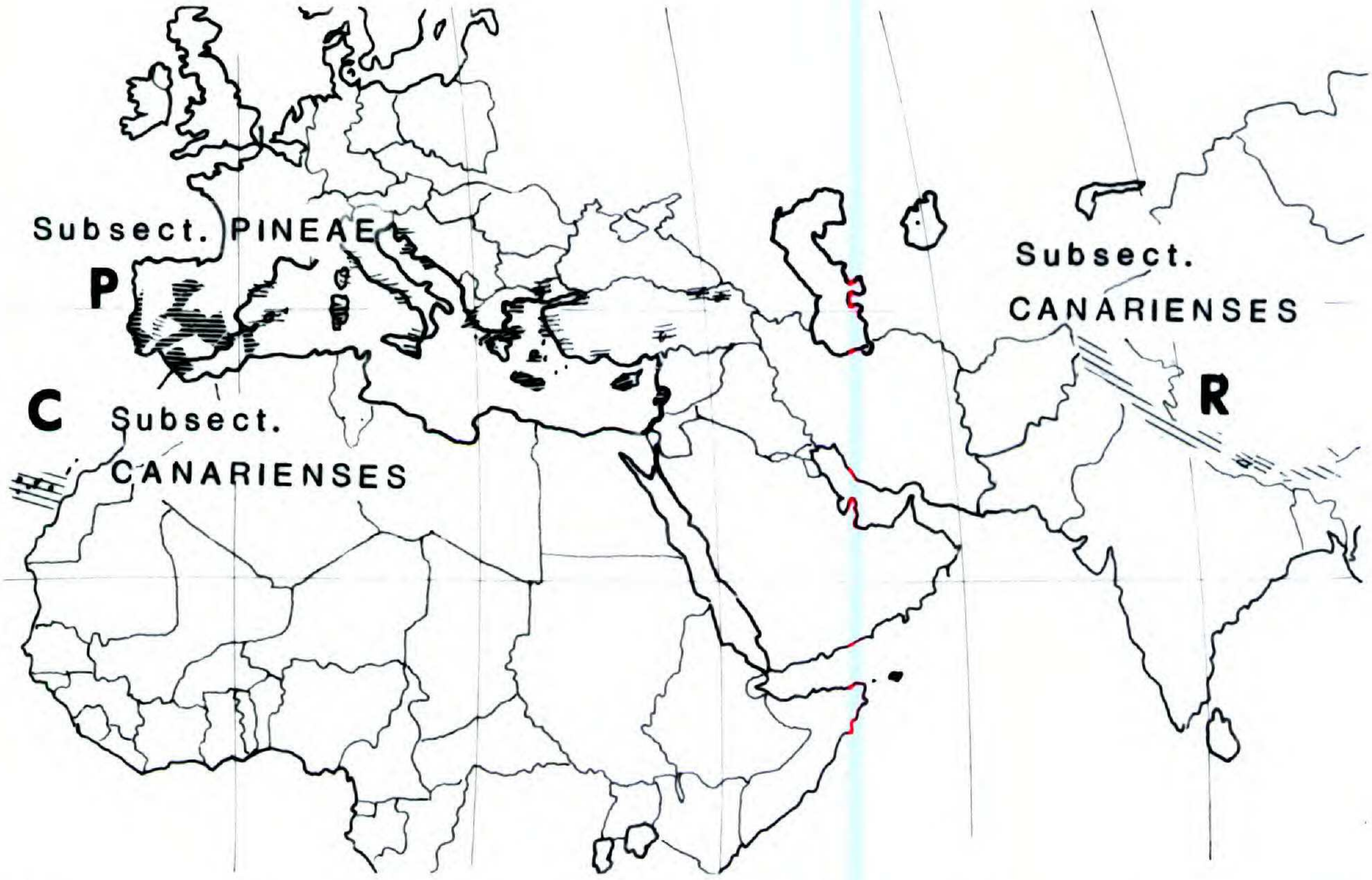


TEXT-FIGURE 5. In Sect. *Strobus*, Subsect. *Strobi* has eight species in Eurasia (E—*P. peuce*, G—*P. griffithii*, A—*P. armandii*, P—*P. parviflora*, F—*P. fenzeliana*, D—*P. dalatensis*, M—*P. morrisonicola*, and W—*P. wangii*), whereas there are six species in North America (S—*P. strobus*, M—*P. monticola*, F—*P. flexilis*, L—*P. lambertiana*, St—*P. strobiformis*, A—*P. ayacahuite*). Note that *P. strobus* is also in southern Mexico (Chiapas) and Guatemala.

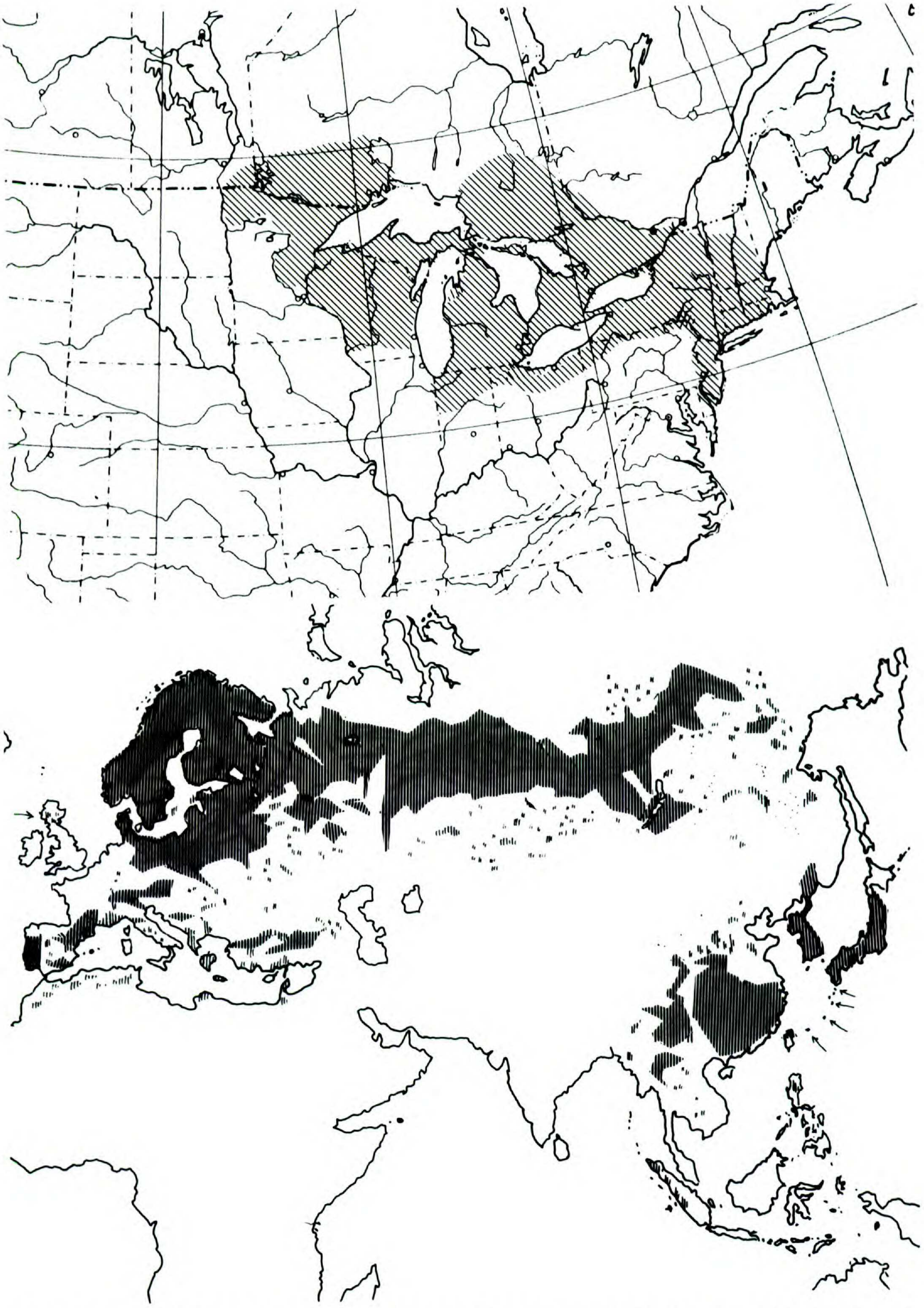


TEXT-FIGURE 6. In Sect. *Parrya*, Subsect. *Cembroides* has eight species in southwestern North America (*P. edulis*, *P. cembroides*, *P. monophylla*, *P. quadrifolia* in the United States; *P. culminicola*, *P. maximartinezii*, *P. pinceana*, *P. nelsonii* in Mexico). Subsect. Gerardiana has two species (G—*P. gerardiana* in the Pamir region, B—*bungeana* in central China), and Subsect. *Balfourianae* has three species (B—*P. balfouriana*, L—*P. longaeva*, A—*P. aristata*) in the western United States.





TEXT-FIGURE 7. In Sect. *Ternatae,* Subsect. *Leiophyllae* with two species (*P. leiophylla, P. lumholtzii*) ranges from southern Arizona-adjacent New Mexico to southern Mexico. Subsect. *Pineae* (one species, P—*P. pinea*) is on the north shore of the Mediterranean Sea. Subsect. *Canarienses* has two species (C—*P. canariensis,* R—*P. roxburghii*) discontinuous from the Canary Islands to the Himalayas. Such disjunctions clearly attest to a long history.



TEXT-FIGURE 8. In Sect. *Pinus,* Subsect. *Sylvestres* with 19 species is largely Eurasian. Only two species are in North America: *P. resinosa* in northeastern USA-adjacent Canada and *P. tropicalis* in Cuba. The alliance has adapted to climates ranging from tropical (Cuba, Vietnam, Sumatra, Phillipines) to Mediterranean, to cold

TEXT-FIGURE 9. Similar cones are produced by *P. albicaulis* and *P. sibirica.* The species differ in that *P. albicaulis* needles are entire, while those of *P. sibirica* are finely serrulate; and *P. sibirica* is a tall tree, *P. albicaulis* is bushy.

asia, appear to be autochthonous as judged from present fossil evidence.

SUBSECT. CEMBRAE

Of the five species in this group, *P. cembra, P. koraiensis, P. pumila,* and *P. sibirica* are in Eurasia, whereas *P. albicaulis* is chiefly at subalpine levels in northwestern North America. Cones of *P. albicaulis* are scarcely separable from those of *P. sibirica* (Text-Fig. 9). The chief differences between these taxa are in the needles (serrulate or not; stomatal position), characters that may have developed following the spread of ancestral taxa into the separate land areas. The age of the ties between these taxa is not known, although Tertiary cones from Eurasia have been compared with *P. cembra* (Gaussen, 1960: 228) and other species (e.g., *P. koraiensis*) reportedly have allied taxa in the Paleogene (Gaussen, 1960). Since fossil records indicate that a *cembra-sibirica*-like pine was present in the Paleogene of Eurasia, an ancestral species allied to them, and to *P. albicaulis,* probably ranged earlier across boreal regions to give rise to separate species in each area, with *cembra-sibirica-pumila* representing chiefly

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temperate in northern Europe and Asia where it reaches above Lat. 60°. Its occurrence in diverse climates in America implies different times of entry, probably Early Paleogene-Late Cretaceous for the ancestor of *P. tropicalis,* as compared with Miocene for *P. resinosa* in northeastern U.S. and Canada.

TEXT-FIGURE 10. Cones of *P. griffithii* from the Himalayas are quite similar to those of *P. monticola* of western North America.

varietal differences across Eurasia. Whereas *P. albicaulis* is a small bushy tree in most of its area, the Eurasian *cembra-sibirica* commonly form tall forest trees. *Cembrae* have a wide occurrence in eastern and central Asia as compared with their restricted areas in the Alps and western North America (see maps in Critchfield & Little, 1966). Since the latter areas were largely under ice sheets during the Quaternary, glaciation may account for these present restrictions as well as the absence of *Cembrae* from eastern North America.

SUBSECT. STROBI

Modern species of this alliance are now Holarctic in occurrence. In North America are *P. strobus* (northeastern U.S.-Canada), *P. strobus* var. *chiapensis* (southern Mexico-Guatemala), *P. monticola* (California-Washington-Idaho-British Columbia), *P. lambertiana* (Baja California Norte, California, Oregon), *P. flexilis* (Alberta-New Mexico-eastern California), *P. strobiformis* (southern Rocky Mountains-northern Mexico), *P. ayacahuite* (southern Mexico-Guatemala). The Eurasian taxa are widely scattered as shown by *P. peuce* (Balkans), *P. armandii* (central China), *P. griffithii* (Himalayas), *P. parviflora* (Japan), *P. morrisonicola* (Taiwan), *P. fenzeliana* (Hainan), *P. wangii* (S. Yunnan), and *P. dalatensis* (Vietnam). Since fossil cones of the general sort produced by these pines are in the Late Cretaceous (some may be *Pityostrobus*), the intercontinental links are old. The occurrence of numerous, presently Asian taxa in North America in Paleocene to Miocene floras (e.g., *Ailanthus, Cercidiphyllum, Ginkgo, Glyptostrobus, Cunninghamia, Metasequoia, Phoebe*) suggests that in favorable montane areas, ancestral *Strobi* populations probably extended across both the Beringian and mid- to North Atlantic regions, thence diverging into allied species as they spread southward on each landmass.

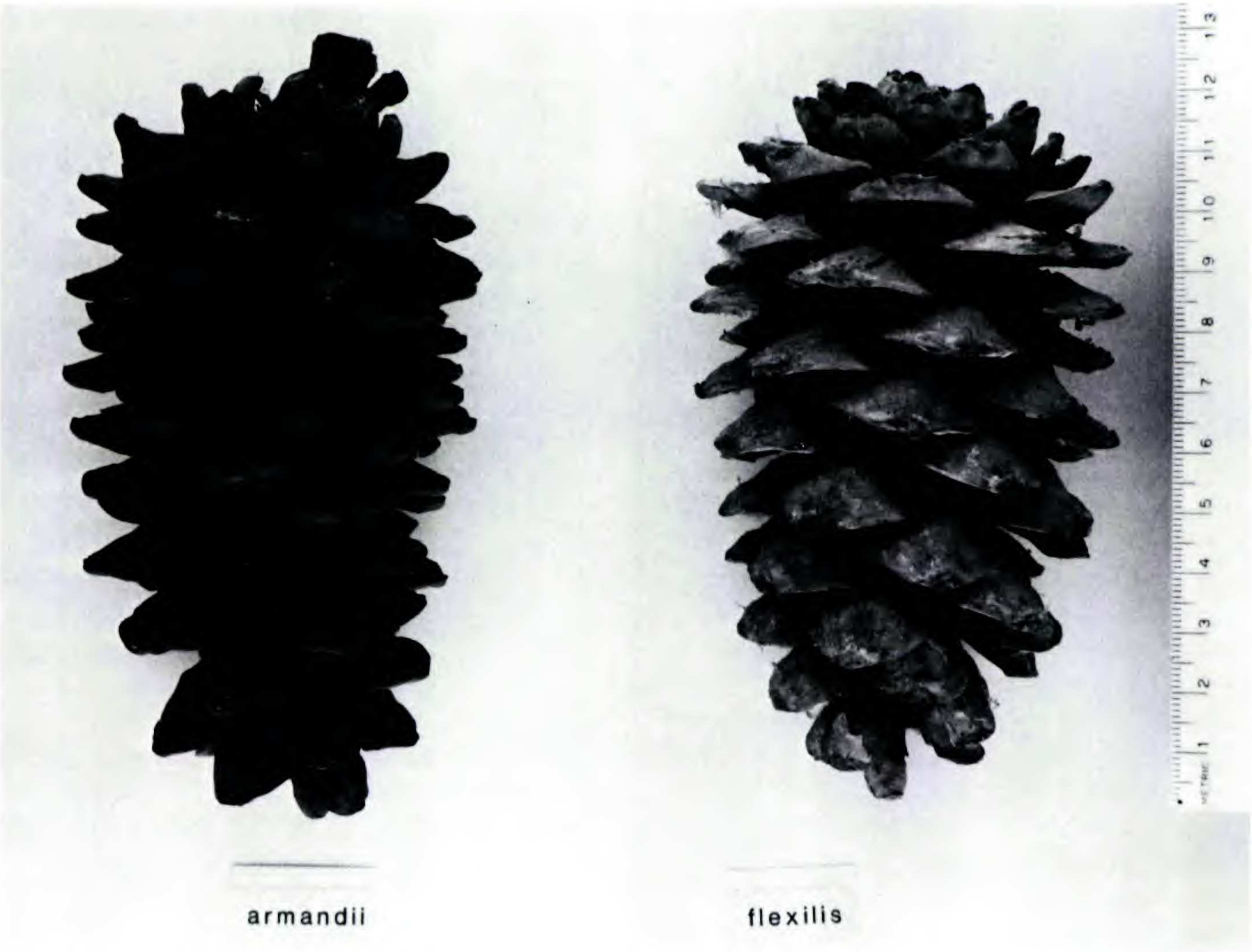
The white pines, *P. strobus* and *P. monticola,* of eastern and western North America are paired-species, and these are allied also to the Himalayan *P. griffithii* (Text-Fig. 10). Both alliances may represent species of an ancestral population that spread south into each landmass and then diverged into related species east and west. This inference is supported by the internal structure of needles of *P. similkameenensis* (Miller, 1973; Stockey, 1984), preserved in cherts of Middle Eocene age near Princeton, British Columbia. This 5-needled pine is referable to Sect. *Strobus,* showing that the alliance was already in the Rocky Mountains 47 Ma ago. This implies that an early Paleogene (or older) link between allied intercontinental species may be inferred because needles of different *Strobi* species are indistinguishable in X-sectional anatomy (Harlow, 1931).

Reports that the American *P. monticola* has a fossil record in Siberia (Mirov, 1967; Wolfe & Leopold, 1967) are unsubstantiated. The cone of *P. monticola fossilis* (Sukachev, 1910) from the Pliocene is more robust and has larger, thicker cone scales, and is not so slender as *P. monticola* cones that are closed (from immersion in water) like the Siberian fossils. A similar, more complete cone is *P. itelmenorum* Vassek. from the Mammoth Mountain flora of Middle Miocene age on the Aldan River (Dorofeev, 1969). Both fossil species are more nearly allied to *P. armandii* from the uplands of central China.

Pinus flexilis from the western interior seems allied to *P. armandii* of central China, which also inhabits cooler montane areas (Text-Fig. 11). An ancestral population may have spread south in the interior, giving rise to paired taxa that diverged chiefly in needle structure (entire or serrate; position of stomata) and seed wings (absent in *P. armandii,* attached to cone scale in *P. flexilis*) in each region. This would have been early, for *P. florissanti* Lesquereux (cf. *P. flexilis*) is in the Florissant flora, Colorado (MacGinitie, 1953), dated at 34 Ma (Epis & Chapin, 1975).

The preceding links between North American and Eurasian white pines follow Shaw's (1914, 1924) reclassification of his *Cembra* Groups (*Cembrae, Flexiles* and *Strobi*) into *Cembrae* and *Strobi.* Species of these morphologic alliances differ in chemical composition of their turpentines (Mirov, 1953, fig. 1). This is expectable for, as suggested for the differences in needle structure, the chemical differences may also have developed as the early populations spread into each landmass.

The Cordilleran white pines, *P. flexilis-strobiformis-ayacahuite,* that stretch from the Canadian Rockies into Guatemala, seem to form a natural series. The question arises as to whether the Eocene (ca. 48–47 Ma) *P. delmarensis* Axelrod from near San Diego, which was then opposite Guaymas, Mexico (Gastil & Jensky, 1973), may be a part of this alliance. Its present position results from displacement northward as the San Andreas rift system was activated, separating *P. delmarensis* from any Mexican connection (Text-Fig. 12). Although *P. delmarensis* seems closely allied to *P. lambertiana* of California, genetic studies indicate that *lambertiana* crosses with Asian pines (*P. armandii, P. koraiensis*), not with American taxa (Mirov, 1967: 334). Since crossing experiments with the Mexican taxa are incomplete (W. B. Critchfield, pers. comm., May 1984), the data are insufficient now to resolve the problem. Structurally, *P. delmarensis* seems closely allied to *P. lambertiana* and may represent an early, western segregate of a group that gave rise to *P. strobiformis-ayacahuite* in the interior. The suggested affinity is supported by the occasional occurrence of moderately reflexed cone scales in *P. lambertiana,* a feature typical of *P. strobiformis* and *P. ayacahuite* cones (Text-Fig. 13). Furthermore, all these taxa have broadly ovate seed wings with rounded tips, not



TEXT-FIGURE 11. Judging from their similar cones, *P. armandii* and *P. flexilis* appear to be paired species. They differ in that *P. armandii* has finely serrulate needles, whereas those of *P. flexilis* are entire. *Pinus armandi* seeds are wingless, and those of *P. flexilis* have the seed wings attached to the scales.

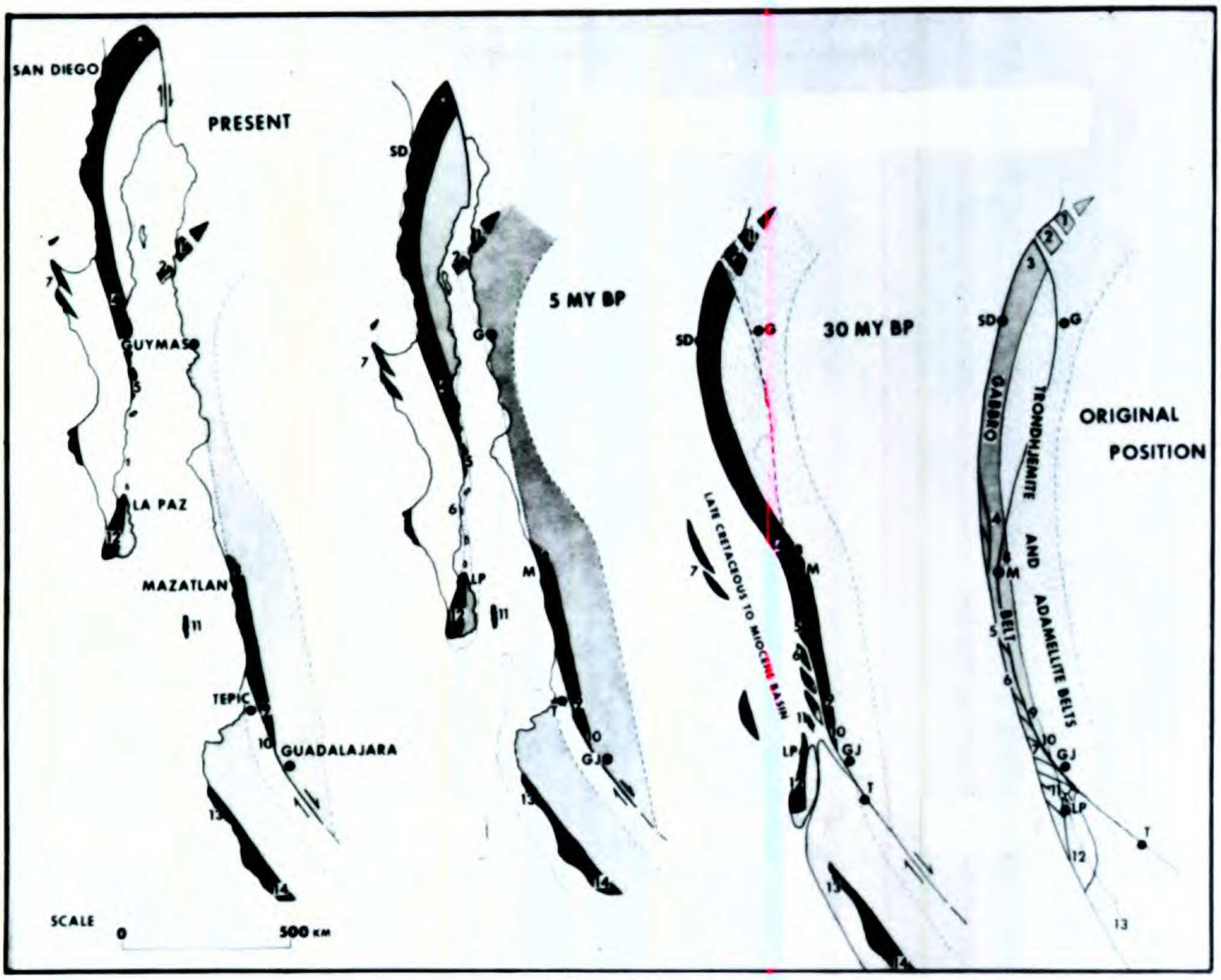
slender wings with acute tips as in *P. monticola* and *P. strobus.*

SUBSECT. CEMBROIDES

Records of this alliance occur in the mid-Eocene Green River flora (47 Ma) of northern Colorado-adjacent Utah (MacGinitie, 1969), and in the Late Oligocene Creede flora (26.5 Ma), southwestern Colorado (Axelrod, unpubl. data). Younger records are in the mid-Miocene Tehachapi flora (17 Ma) of the western Mohave region (Axelrod, 1939), the Stewart Spring flora (13 Ma) of southwestern Nevada (H. Schorn, pers. comm.), and in the Chalk Hills Formation (5–6 Ma) near Bruneau, Idaho (Knowlton, 1901; Brown, 1940; Malde & Powers, 1962). That *Cembroides* do not hybridize with other pines (Mirov, 1967: 569) and have been in existence since the Eocene, demonstrates that it is a very distinct subsection. This is suggested also by the observation that the woods of nut-pines have piciform lateral ray pits and thick-walled ray cells that approach in structure those of Cretaceous "pines" (Bailey, 1910).

The fossil piñons were chiefly subordinate members of rich woodland vegetation, whereas they now often dominate woodlands. The Idaho occurrence of *Pinus lindgrenii* Knowlton near Bruneau may be an exception. A number of cones have been recovered by local collectors, and a dozen or so are in the Jurupa Museum, Riverside. Their relative abundance suggests that Piñon may have had at least a subordinate role in the flora. This is consistent with their worn, eroded nature, which indicates transport, presumably from a piñon zone that covered warmer, south-facing slopes bordering the floodplain.

With respect to *Pinus cembroides* var. *cembroides,* the question may be raised as to whether *P. cembroides* var. *lagunae* Robert-Passini (1981) may not be the most ancient living member of the species. As described further by Bailey (1983), it differs from *P. cembroides* var. *cembroides* in



TEXT-FIGURE 12. Disruption of western Mexico and its northward displacement following 25 Ma ago (from Gastil & Jensky, 1973). Members of several *Pinus* subsections were displaced northward into the developing Mediterranean climate of California and border area.

its average longer needles, thinner fascicles, fewer stomatal lines, longer cone peduncles, and more obvious prickles on the umbos. In addition, I have noted that the trees are more robust and larger than *P. cembroides* var. *cembroides,* and the cones are larger than those of most populations in the Southwest and northern Mexico.

The var. *lagunae* inhabits uplands of the Cape Region, Baja California. The limited (10 year) record at La Laguna indicates a mean annual temperature of 14.5°C and an annual range of 7.5°C (Garcia, 1973). This gives the area a very equable climate—*M* 65 in Bailey's (1960, 1964) classification. The pine is a component of the piñon-madrone evergreen-oak woodland at altitudes generally from 1,600 to 2,000 m. The notion of its antiquity is consistent with the occurrence of other marked endemics or disjunct taxa in the area, notably *Garrya salicifolia, Populus brandegeei, Quercus albocincta, Q. devia, Q. rugosa, Q. tuberculata, Rhus tepetate,* a feature shown by upland floras of other insular regions (Cedros Island, Canary Islands, Revillagigedo Islands, Madeira Islands, Juan Fernandez Islands, and others). The Cape Region was isolated from the mainland following 25 Ma ago (Text-Fig. 12), and the Gulf opened about 5–6 Ma ago, as judged from sea-floor spreading anomalies (Gastil & Jensky, 1973). Persistence of relict taxa in the uplands there thus seems understandable from both a geologic and climatic standpoint. The differences between *P. cembroides* var. *lagunae* and other taxa of the *cembroides* complex (see Bailey, 1983; Bailey & Hawksworth, 1979, 1983; Bailey & Wendt, 1979; Little 1966, 1968; Robert-Passini, 1981), involve their shorter needles, thicker fascicles, and other features that presumably reflect more recent adaptation to increasing aridity in areas bordering the Mexican plateau.

SUBSECT. BALFOURIANAE

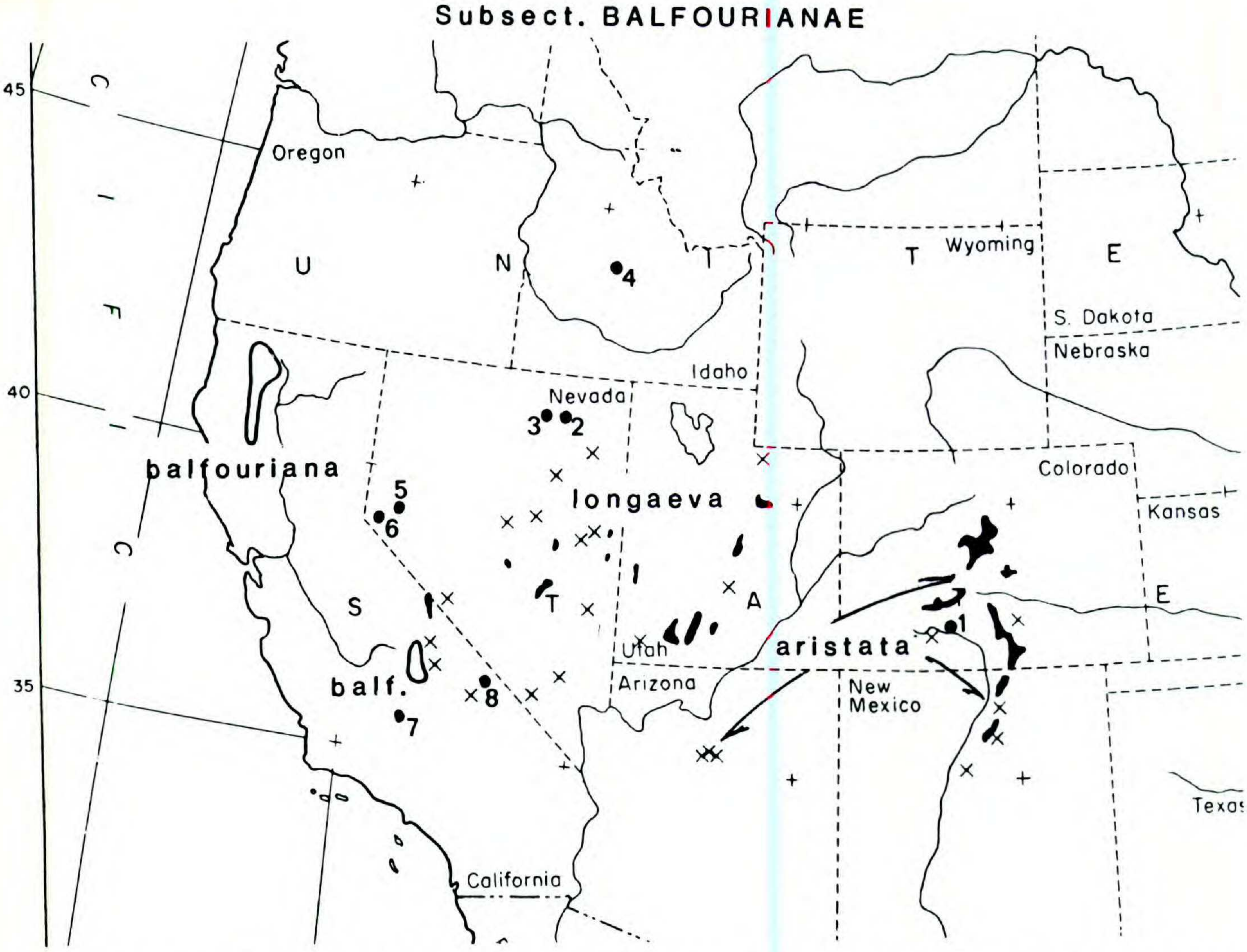
This small alliance includes three taxa, *P. aristata* Engelm. of Colorado-northern New Mexico and northern Arizona, *P. longaeva* Bailey of Utah and the Great Basin, and *P. balfouriana*

TEXT-FIGURE 13. *Pinus lambertiana* is allied to *P. delmarensis* from Middle Eocene rocks near San Diego. The Californian taxa were isolated from the related Mexican *P. strobiformis-ayacahuite* by movement on the San Adreas rift system.

Murray, which is disjunct in California from the Klamath Mountain region to the southern Sierra Nevada, 625 km (390 mi.) distant. Their detailed distribution is charted by Bailey (1970, fig. 3).

There are fossil records of two of these taxa (Text-Fig. 14). *Pinus aristata* is scarcely separable from *P. crossii* Knowlton from the Creede flora (26.5 Ma), Colorado, where the branches of *P. aristata* overhang some of the fossil sites today. *Pinus crossii,* abundantly represented at Creede by cones, foliage, and winged seeds, lived adjacent to a rich piñon-juniper woodland, a community usually well removed from *P. aristata* today. Cones and foliage of *P. crossii* are also in the Hillsboro flora, central New Mexico, dated at 32 Ma. Its associates included spruce and several rare, small leaflets of *Mahonia.* This appears to have been a high montane site with a rich, or nearly pure, stand of fossil bristlecone pine (Axelrod & Bailey, 1976). A species allied to *Pinus crossii* was already in existence in the Late Eocene (40 Ma), as judged from winged seeds and a fascicle in the Copper Basin flora (Axelrod, 1966a), which represents a rich conifer-hardwood forest. This species also contributed to pure montane conifer forests in the Late Eocene Bull Run flora north of Elko, Nevada.

The distal half of a cone in the Lower Oligo-

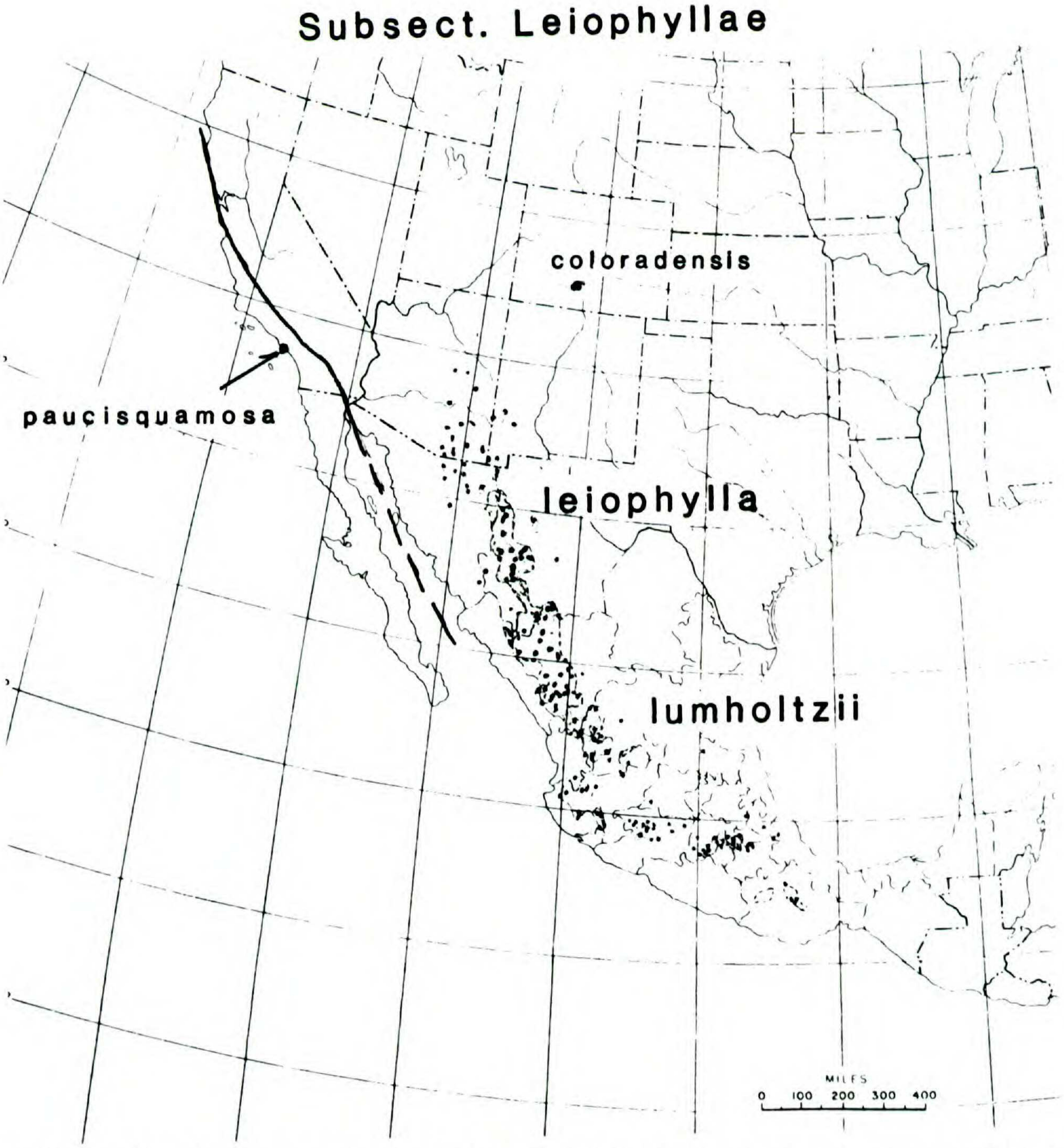

Subsect. BALFOURIANAE

TEXT-FIGURE 14. Distribution of the three species of Subsect. *Balfourianae* (map from Critchfield & Little, 1966): *P. aristata, P. longaeva,* and *P. balfouriana.* Fossils of *P. crossii* Knowlton, allied to *P. aristata,* occur at 1—Creede, 2—Copper Basin, 3—Bull Run. *Pinus balfouroides* Axelrod, allied to *P. balfouriana,* is recorded at 4—Thunder Mt., 5—Purple Mt., 6—Chalk Hills, 7—Sharktooth Hill, and 8—Death Valley. Fossils related to *P. longaeva* are not now known.

cene (Chadronian) Titus Canyon Formation (Stock & Bode, 1935), Death Valley, appears to be *P. crossii.* Its affinity is suggested by the thin cone scales surmounted by low, near-terminal umbos, and by the generally ovate shape of the partially open cone. Its Early Oligocene occurrence in the southern Great Basin, as well as in northeastern Nevada in the Late Eocene, suggests that *P. crossii* probably originated in the western interior.

Pinus balfouroides Axelrod from the Oligocene Thunder Mountain flora, Idaho (in Brown, 1937), is represented by relatively large cones (+9 cm), as well as needles in 5s. Another Idaho record is in the Coal Creek flora (27 Ma), Lost River Range, where it is also associated with a humid conifer forest, including species of *Abies, Picea, Larix, Pinus, Tsuga, Chamecyparis,* and *Sequoiadendron. Pinus balfouroides* occurs in western Nevada in the Chalk Hills (Axelrod, 1962) and Purple Mountain (Axelrod, 1976b) floras. Dated at 12 and 13 Ma, respectively, the fossils include relatively small cones (6–7 cm long), as well as winged seeds and foliage. A cone is also in the marine Temblor Formation (15 Ma) at Sharkstooth Hill near Bakersfield, where it was transported from the Sierra Nevada into the marine basin.

The few fossil cones available suggest that in size the Thunder Mountain population is more nearly like that now in the Klamath Mountains where *P. balfouriana* var. *balfouriana* occurs, whereas the smaller cones in the western Nevada floras are comparable to the southern Sierran population, *P. balfouroides* var. *austrina* (Mastroguiseppe & Mastroguiseppe, 1980). The larger-coned, northern population, which has been in a more mesic climate since the Oligocene, shifted coastward during the Neogene to the humid Klamath Mountain area. By contrast, the smaller-coned *austrina* may have originated in the subhumid western Nevada region and moved



TEXT-FIGURE 15. Occurrence of species of Subsect. *Leiophyllae* in the past and today (map from Critchfield & Little, 1966). The coastal southern California occurrence of *P. paucisquamosa* Templeton in the Middle Miocene probably reflects displacement northward from Mexico (see Text-Fig. 12). The record of *P. coloradensis* Knowlton at Creede reflects the wider distribution of Leiophyllae in the Late Paleogene, a time when other fossil taxa with relatives now far to the south also ranged widely to the north.

into the southern Sierra Nevada as climate became drier. It survived there largely south of the Pleistocene ice cap. Since the close of the Wisconsin, it has spread some 40 km (25 mi.) north to its present northern area near Onion Valley, above Independence, an area under ice during Wisconsin glaciation.

SUBSECT. LEIOPHYLLAE

Fossil cones of *Pinus coloradensis* Knowlton, and foliage presumed to represent the species, occur in the late Oligocene Creede flora, Colorado. The fossils appear to represent the Leiophyllae, and show relationship to *P. chihuahuana* Engelm., also considered a variety of *P. leiophylla*. The fossil needles in 5s are shorter than those of the modern species. *Pinus leiophylla* ranges today from southeastern Arizona-adjacent New Mexico into southern Mexico (Oaxaca).

The well-preserved cone on *Pinus paucisquamosa* Templeton (1953) that represents this alliance comes from the marine Altamira Shale near Pt. Fermin, at the south end of Palos Verdes Peninsula, southern California (Text-Fig. 15).

Dated at 14.5 Ma, and of early Mohnian age, it was compared initially with *P. chihuahuana.* As judged from the broad cone scales of the fossil, it appears more nearly allied to the only other member of this alliance, *P. lumholtzii* of the Sierra Madre Occidental.

As with several other taxa, this record may have been transported to its present area by movement along the San Andreas rift system. This would place it at the latitude of northern Sonora in the Middle Miocene, an area close to members of the Leiophyllae today and an area where they probably were also in the past (see Text-Figs. 12, 15).

SUBSECT. SYLVESTRES

This alliance is represented in the Eocene of British Columbia as judged from the internal structure of cones and foliage preserved in the Allenby Formation (46 Ma) near Princeton (Stockey, 1984). The evidence indicates that cones of *P. princetonensis* Stockey, as well as the cone of *P. arnoldii* Miller and needles of *P. allisonii* Stockey have the characteristics of Subsect. *Sylvestres.* This suggests a Beringian connection with Eurasian members of the alliance in the Early Eocene or Paleocene.

The cones of *P. clementsii* Chaney (1954) from the Late Cretaceous (85–86 Ma) of southern Minnesota were compared by Mirov (in Chaney) with the living *P. resinosa* Aiton. However, the preservation of the mold that represents the holotype (Chaney, 1954, figs. 1, 2) is poor, and the features of the umbo are not clear. The paratype (Fig. 6) is an incomplete specimen, and neither specimen has internal structure preserved. These specimens, from localities 40 km (25 mi.) apart, appear to be different species. They may represent the genus *Pityostrobus.*

SUBSECT. AUSTRALES

The 11 species of this group are now in eastern and southeastern North America. As based on genetic data resulting from numerous hybridization tries, Critchfield (1962) concluded that the group is a natural one. The few taxa that do not cross readily are either removed from the others by geographic distance or in "flowering" time.

The oldest fossils that may be allied to this group are the Paleocene *Pityostrobus* (*Pinus*) *lynni* (Berry) Miller (Berry, 1934; Miller, 1977b) and the Middle Miocene *P. collinsi* Berry (1936, 1941). Both are similar in external features to cones of *P. taeda* L. Miller (pers. comm., 1984) pointed out that *P. avonensis* Miller (1969), *P. buchananii* Underwood & Miller (1980), and *P. driftwoodensis* Stockey (1983) all belong to either *Australes* or *Ponderosae,* though it is not now possible to determine which one group they may represent. (see Stockey, 1984, table 1).

Species allied to Australes have been described from the Neogene of western Europe, including fossil pines similar to *P. taeda, P. pungens,* and *P. rigida* (Gaussen, 1960: 234). The illustrations generally resemble these pines, but a final decision must be based on a reexamination of the fossils themselves. That the records may represent species of Australes would be consistent with the Neogene record in western Europe, where many species allied to those now in the eastern United States occur. Among these are species of *Acer, Betula, Carya, Diospyros, Fagus, Hamamelis, Juglans, Lindera, Liquidambar, Nyssa, Persea,* and *Quercus,* as well as the conifer *Taxodium.* Some of them occur in intermediate areas, notably in the Miocene of Iceland (Akhmetiev et al., 1978; Heer, 1968; Moorbath et al., 1968). If *Australes* pines were in western Europe, they presumably were eliminated there along with the now-American hardwoods and swamp cypress during the later Pliocene and Pleistocene as cold and then ice spread southward. The presently-American (and Asian) taxa were blocked from southward retreat by the elevated Alpine axis that stretches across southern Europe and thus became extinct there.

SUBSECT. PONDEROSAE

Regarding the possible antiquity of this alliance, the recent description of well-preserved, silicified *Pinus* wood from the base of the early Upper Cretaceous Eutaw Formation (basal Coniacian), northeastern Mississippi, is of considerable interest (Blackwell, 1984). The wood is reported most similar to that of Subsect. *Ponderosae* (cf. *P. ponderosa*) though some of its features suggest relationship with woods of the allied Subsect. *Australes* (cf. *P. taeda*). *Pinuxylon eutawense* Blackwell may represent a pine ancestral to Subsect. *Australes,* or possibly to *Ponderosae* as well. In any event, yellow pines are clearly foreshadowed at this early date (ca. 88 Ma ago), as is indicated also by the cone of *Pityostrobus* (*Pinus*) *lynni* noted above.

Ponderosae fossils are certainly Eocene, as judged from seed-wing records and needles in the Green River (MacGinitie, 1969) and Florissant floras (MacGinitie, 1953). In addition, needles of *P. andersonii* Stockey (1984), preserved in chert of the Allenby Formation (46 Ma) near Princeton, British Columbia, have the internal structure of *Ponderosae* needles. Furthermore, the silicified cone of *P. premurrayana* (Knowlton, 1899), from the east side of Yellowstone Lake, and probably from the early mid-Eocene Langford Formation (ca. 50 Ma, Smedes & Protska, 1972), is also a member of the *Ponderosae*. It is similar to cones of *P. lindleyii* Loudon, now in Mexico and considered by some to be a variety of *P. montezumae* (i.e., Martinez, 1948).

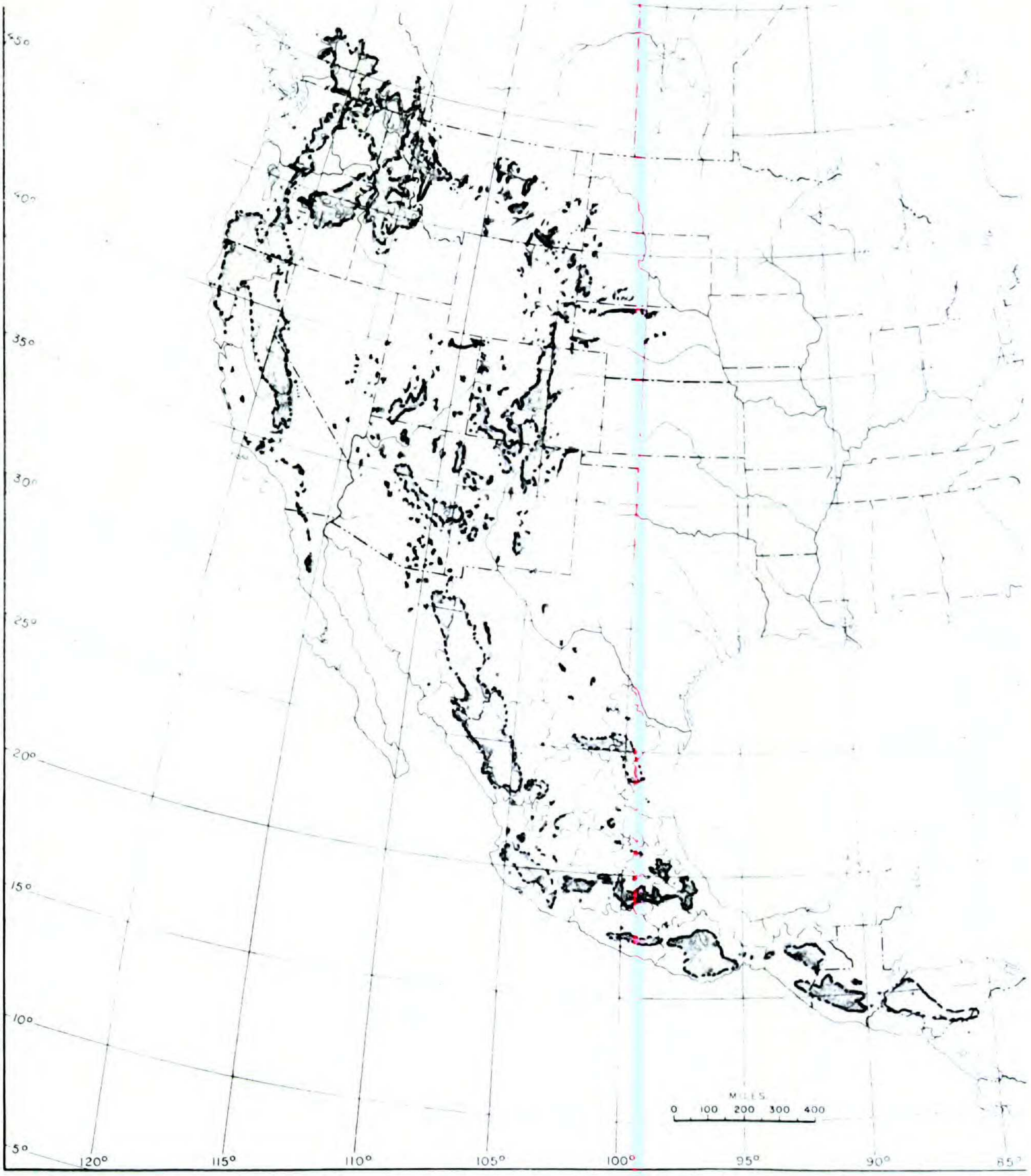
Remains of several *Ponderosae* are in the Late Oligocene Creede flora, Colorado. They resemble those of species now in the Southwest and/or Mexico, notably *P. chihuahuana, P. engelmannii, P. michoacana,* and *P. montezumae.* This suggests that the southern Cordilleran region that extended southward into Mexico was a major center for diversification of *Ponderosae* in the Paleogene. Its species probably were restricted southward gradually as colder climate spread over the central and southern Rocky Mountains, leaving *P. scopulorum* the chief survivor, and with *P. engelmannii* and *P. arizonica* reaching their northern limits in southern Arizona and adjacent New Mexico, a region of warmer climate (see Axelrod & Raven, 1985, figs. 5, 6). The remaining *Ponderosae* (e.g., *P. cooperi, P. douglasiana, P. durangensis, P. hartwegii, P. lawsonii, P. michoacana, P. montezumae, P. pseudostrobus, P. tecote*) now occur well south of the U.S.-Mexican border, or in California-Oregon (*P. jeffreyi, P. ponderosa, P. washoensis*).

A northwestward occurrence of a presently Mexican and Southwestern *Ponderosae* in the Miocene is indicated by *P. truckensis* Axelrod. It occurs in rocks 12.5 Ma old in the Truckee River drainage east of Reno, at Celetom diatomite quarry. The large asymmetrical cone is similar to those produced by *P. pseudostrobus.*

During the Middle and Late Miocene, branchlets, needles, and seed-wings similar to those produced by *P. ponderosa* occur at a number of sites in western Nevada, including the Eastgate, Fallon, Fingerrock, Middlegate, Stewart Spring, Pyramid, and Verdi floras. These are chiefly forest-border assemblages that lived for the most part under subhumid climate. By contrast, it is evident that *P. ponderosa*-like structures are largely absent in the floras of Oregon, Idaho, and Washington that occupied more humid climates.

Pinus ponderosa (including its varieties) has a broad range, reaching from southern British Columbia to San Luis Potosí, Mexico, a distance of 3,850 km (2,350 mi.). As noted by Critchfield and Little (1966: 16), it is absent from a large part of the intermontane region, notably southern Idaho, western Wyoming, southwestern Montana, and a good part of the Great Basin ranges of northern Utah and much of Nevada (Text-Fig. 16). However, fossil records show that *ponderosa*-like structures (needles, winged seeds) occurred in the region; the general rarity of fossils in the eastern part of the area reflects the fact that the rocks there are chiefly of Mesozoic and older formations.

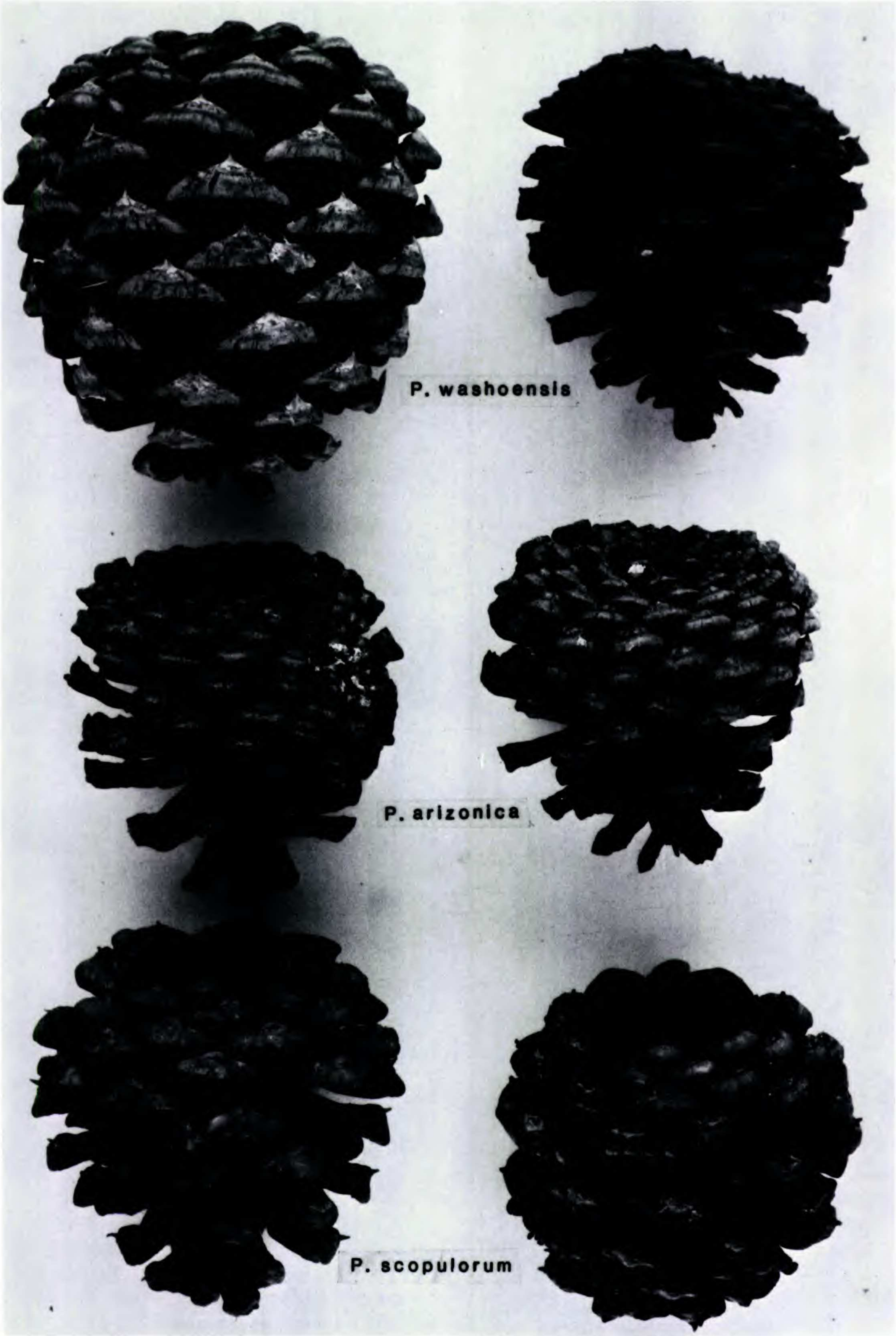
The present absence of *P. ponderosa* from much of the intermontane region may be explained by several factors (Axelrod, 1976a). In the first place, precipitation over most of the lowland region totals less than 250 cm (10 in.) and hence is insufficient to support these trees. The pine has a normal growing season from May through August. Since precipitation is low, seedlings cannot become established readily because adequate soil moisture is critical for establishment (Fowells, 1965). In this regard, *P. ponderosa* (*scopulorum*) does occur in the eastern Great Basin ranges, where late spring–summer rains are frequent. Pines that may have survived in the isolated ranges following the last glaciation probably were eliminated there by the post-glacial Xerothermic period. Increased summer evaporation rate would have been a critical factor in eliminating pine seedlings. Furthermore, trees probably could not survive by retreating upslope to moister areas because climate there is too cold in summer. In addition, aspen outcompetes pine in the same zone and may partly account for its absence over much of the region. An aspen-sage-meadowland association forms the zone in which pine would occur naturally (Axelrod, 1976a). Aspen competes with pine for water, but aspen, with its shallow, spreading roots, outcompetes pine seedlings. Aspen not only spreads rapidly by suckers in its early years (Fowells, 1965), it is also intolerant of shade, as is ponderosa pine. Hence, aspen competes further with pine seedlings if they are present. Under present conditions, the aspen-sage-meadowland zone is a relatively permanent drought-resistant vegetation type in the inter-



TEXT-FIGURE 16. Of the 12–13 species of Subsect. *Ponderosae,* only three occur north of southern Arizona (i.e., *P. ponderosa* with two vars., *P. jeffreyi, P. washoensis*). Note the broad area in the intermontane region where *ponderosa* does not now occur (see text for discussion).

montane region, occupying areas where *P. ponderosa* might exist if precipitation was higher.

The origin and relationships of *Pinus washoensis* Mason & Stockwell (1945) provide a noteworthy problem. The species occupies a continental climate and occurs in the upper mixed-conifer forest and in the fir forest. It is scattered discontinuously from the east slope of the Carson Range, Nevada, northward into British Columbia. The species is characterized by small, compact, ovate cones. Haller (1959, 1965, 1984) concluded that it is allied to populations of *P. ponderosa* ranging from the Lake Tahoe region northward through eastern Oregon into interior British Columbia. He noted that in its type area, where it is quite distinct, it only crosses with *P. ponderosa* with reduced seed set. It becomes less distinct northward and gradually tends to merge with the northern *P. ponderosa* populations. These hybrids are quite variable, suggesting that hybridization between the Rocky Mountain and Pacific races of *P. ponderosa* has played a role in


P. washoensis
P. arizonica
P. scopulorum

their origin. Haller concluded that *P. washoensis* may be a segregate from these hybrids maintained in isolation at the south, but only partially differentiated in the north where distribution is more continuous.

However, there appears to be evidence for its relict nature. This is implied by breeding studies that show that it crosses most readily with Rocky Mountain (Colorado-Black Hills) populations of *P. scopulorum* Engelm. and with which it produces most seeds (Critchfield, 1984a). Further, in terms of its seed proteins, the pine in its type area on Mount Rose has an antigenic distance of 0.6 from the Sierran ponderosa pine (Prager et al., 1976). This is greater than the distance between *P. jeffreyi* and *P. sabiniana* (0.4–0.5), although less than the values from *P. coulteri* and *P. engelmannii* (0.8–1.9) (Prager et al., 1976). The data presented by Critchfield (1984a) suggested that separation from an ancestral population may have occurred on the order of 20–30 Ma ago. This is possible since the remains of *P. ponderosa-scopulorum*-like pines occur in the Eocene and Oligocene. Critchfield also pointed out that in the ability of Washoe pine to cross with other taxa, it "behaves like a fragment of the Rocky Mountain race stranded at the west edge of the Great Basin."

To follow up this suggestion, I examined stands of *P. scopulorum* in eastern Nevada, western Utah, and southern to central Colorado and Arizona. In the last two areas, especially, the cones are generally similar to those produced by *P. washoensis* but are not so compact. They differ in that *P. scopulorum* cones are ovate, whereas those of *P. washoensis* are ovate-rotundate (i.e., rounded or globate), *P. washoensis* has more numerous scales (173 vs. 112–141); in cone color (purple vs. green for *P. scopulorum*); wing length (shorter vs. longer in *P. scopulorum*); and longer seeds in *P. washoensis* than *P. scopulorum* (Critchfield, 1984a).

Further evidence for a Cordilleran source for *P. washoensis* is provided by *P. arizonica* Engelm. of southern Arizona, adjacent New Mexico, and northern Mexico. This tree regularly produces small, compact, ovate-rotundate cones scarcely separable from those of *P. washoensis* (U.C. Herb. 335574, 334313—Santa Catalina Mts., 334316 Chiricahua Mts.; also see Shaw, 1909, pl. 17, fig. 4). The long needles are in fascicles of 3s and 5s, expectable in warmer regions where pines commonly have more needles (Shaw, 1914; Mirov, 1967). The similarities suggest that *P. washoensis* may have been derived from a population closely allied to *arizonica-scopulorum* (Text-Fig. 17). This implies that a population with generally small, globose cones ranged across the Great Basin during the Neogene. It may have originated during the later Middle Miocene (ca. 13–12 Ma) as climate rapidly became drier and numerous exotics disappeared from that region (Axelrod, 1985). Adaptation to increasing summer drought in the west presumably resulted in the development of somewhat more compact cones and shorter needles commonly in 3s, as seen in *P. washoensis.*

The suggestion that *P. washoensis* may be a relict population derived from a Cordilleran source is consistent with paleobotanical evidence. A number of basically Rocky Mountain and intermontane taxa now range across the Great Basin to the Sierra Nevada and border areas (see Little, 1971, 1976). Among these, the following have equivalent species in the Miocene floras from the present desert area of western Nevada:

Acer diffusum
Alnus tenuifolia
Amelanchier utahensis
Betula fontinalis
Celtis reticulata
Cercocarpus ledifolius
Elaeagnus velutina
Holodiscus dumosus
Juniperus osteosperma
Paxistima myrsinites
Peraphyllum ramosissimum
Pinus monophylla
Pinus ponderosa
Populus angustifolia
Prunus demissa
Prunus emarginata
Ribes cereum
Symphoricarpos oreophilus

Others with this distribution that do not now

←

TEXT-FIGURE 17. Cones of *Pinus washoensis* (from Mt. Rose, Nevada, alt. 2,430 m [8,000 ft.]), *P. arizonica* (from Huachuca Mts., Arizona, alt. 2,130 m [7,000 ft.] and *P. scopulorum* (from Creede, Colorado, alt. 2,675 m [8,800 ft.]) are so similar they indicate that these are closely related taxa. The suggestion that *P. washoensis* is a relict, Cordilleran taxon is supported by paleobotanic and genetic evidence (see text).

have a known fossil record in Nevada include *Chamaebatiaria millefolium, Pinus flexilis,* and *P. longaeva.*

Neogene floras of western Nevada, and also of central California, have a number of trees and shrubs allied to those in the southern Rocky Mountains, and some are represented by species only in Mexico. Among these are fossil species allied to:

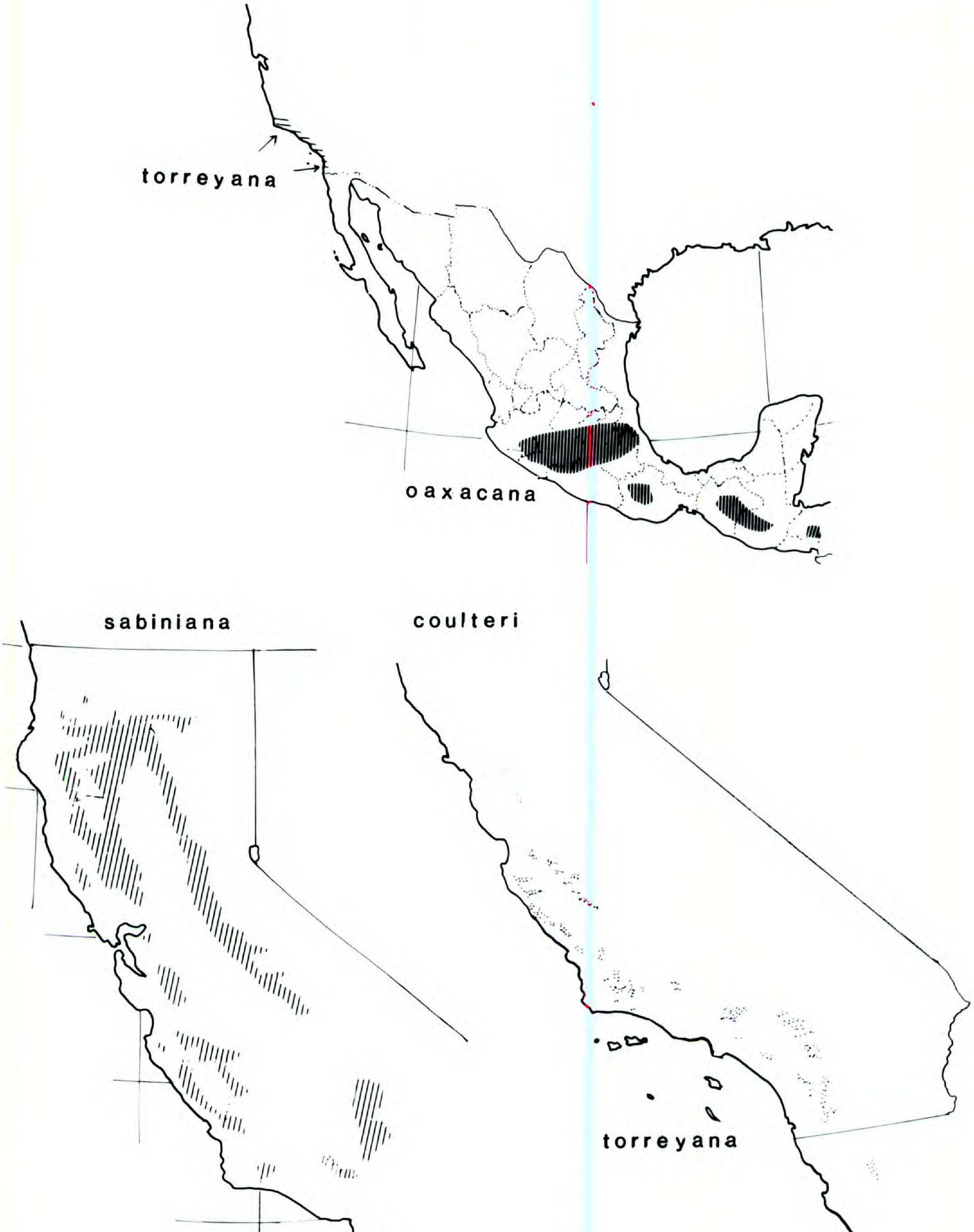
Acer grandidentatum
Arbutus arizonica
Bumelia lanuginosa
Cercocarpus breviflorus
Crataegus erythropoda
Fraxinus anomala
Juglans major
Populus brandegeeii
Populus mexicana
Quercus arizonica
Quercus vaseyana
Robinia neomexicana
Sapindus drummondii

Fossil species of the above taxa contributed to mixed conifer forest, sclerophyll woodland, and juniper woodland, together with species allied to those now in California. The Cordilleran and Madrean taxa that occupied the present Great Basin during the later Miocene were largely eliminated there as summer rain decreased further in the Pliocene (Axelrod, 1976a). Relict stands occur now in the higher mountains bordering the eastern Great Basin where there is more summer precipitation, as well as along the eastern slope of the Sierra Nevada and bordering ranges where such typical "Rocky Mountain" taxa as *Pinus flexilis, Populus angustifolia,* and others still occur. In sum, the evidence seems compatible with the view that *P. washoensis* may be a relict Cordilleran pine, one derived from a plexus allied to *P. scopulorum* and *P. arizonica.*

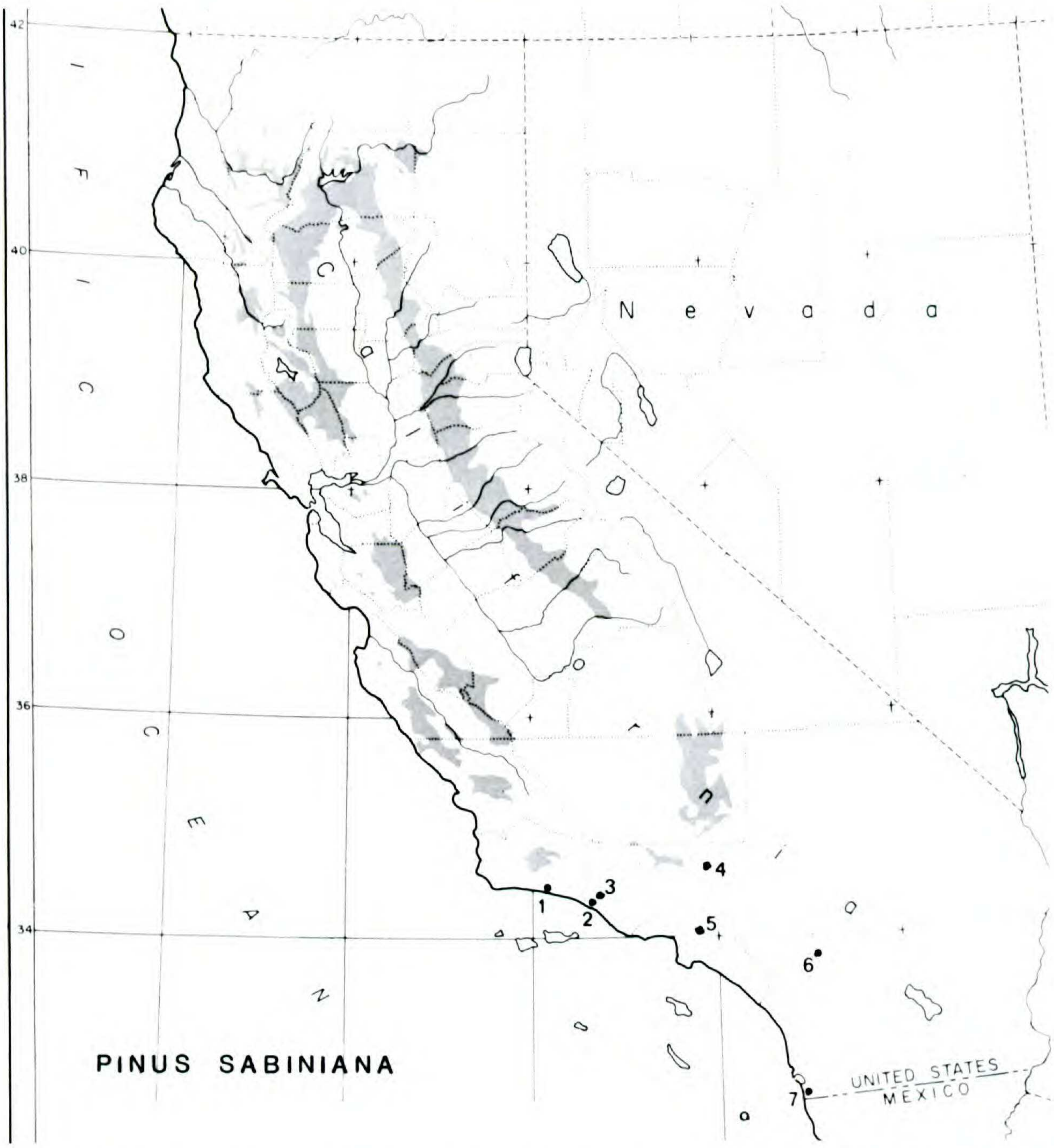
SUBSECT. SABINIANAE

This small group of three pines, *P. torreyana, P. sabiniana,* and *P. coulteri,* occurs in California, with *P. coulteri* scattered discontinuously into the mountains of northern Baja California (Text-Fig. 18). The only species with a limited fossil record is *P. pieperi* Dorf, which is allied to, if not identical with, *P. sabiniana.* Confined now to the Coast Ranges and foothills of the Sierra Nevada in central and northern California, all of its fossil records are in southern California (Text-Fig. 19). These include the later Miocene Anaverde (Axelrod, 1950) and Mount Eden (Axelrod, 1937) floras, the Pliocene Chula Vista (Axelrod & DeMéré, 1984) and Pico (Dorf, 1930) floras, the Early Pleistocene Seacliff flora (Axelrod, 1983a), a cone from the Early Pleistocene in Lake Canyon near Ventura (Wiggins, 1951), and a cone scale in the late Pleistocene (Wisconsinian) Carpinteria (Chaney & Mason, 1933) and Rancho La Brea floras (Warter, 1976). *Pinus sabiniana* may have disappeared from southern California during the Xerothermic, which brought a hotter, semi-desert climate to the coastal strip. This climate may also account for the present disjunct occurrences of *P. sabiniana* in central and northern California, where isolated populations often are surrounded by mesic, mixed-conifer forest which spread with cooler, moister climate following the Xerothermic (Axelrod, 1966b: 50).

At present, there is no known fossil record of *Pinus torreyana,* one of the most restricted of pines. A few thousand trees now inhabit the coastal bluffs of Torrey Pines State Park and nearby Del Mar, a few miles north of San Diego, and a subspecies occurs on Santa Rosa Island, 60 km southwest of Santa Barbara (Haller, 1986). The mainland population is near the head of La Jolla submarine canyon. Upwelling of colder water gives this local area a foggier, cooler climate than the adjacent coast and may account for the persistence of *P. torreyana* there (Axelrod, 1982). There is also a highly marine, cooler, foggy climate on Santa Rosa Island. Cones of *P. torreyana* are similar to those of *P. oaxacana* Mirov of Mexico, a species that has long needles in 5s like *P. torreyana* (Text-Fig. 20). Significant in this regard is the occasional occurrence of strongly-hooked apophyses on cones of *P. oaxacana* that simulate those of the *Sabinianae* (specimens in Inst. Forest Genetics, Placerville, California). *Pinus torreyana* may have been derived from a *P. oaxacana*-like pine in western Mexico, which then extended west to include the present area of Baja California. Activation of the San Andreas rift system by the Early Miocene (or earlier?) transported the area, and the pine, northward (see Axelrod, 1980, figs. 7, 8). Fossil species allied to *P. sabiniana* and *P. coulteri* may have had a similar origin at the south but were adapted to interior lowland (*P. sabiniana*) and montane (*P. coulteri*) habitats. The difference in needles, which are more slender and drooping in *P. oaxacana,* and thicker and more rigid in *Sabinianae,* may reflect adaptation to the more xeric environment



TEXT-FIGURE 18. In Sect. *Pinus*, Subsect. *Sabinianae* has three species in California-Baja California, (*P. sabiniana*, chiefly in the interior at lower altitudes in central California; *P. coulteri*, montane in the inner Coast Ranges and southern California-Baja California, and *P. torreyana*, confined to two local areas in coastal southern California). Forerunner of the last may have been displaced northward from an ancestral population allied to *P. oaxacana* now in central to southern Mexico (see Text-Fig. 12).



TEXT-FIGURE 19. Fossil sites for *P. sabiniana* and its ancestor *P. pieperi* Dorf. (map from Griffin & Critchfield, 1972): 1—Carpinteria, 2—Pico, 3—Lake Canyon, 4—Anaverde, 5—Rancho La Brea, 6—Mount Eden, 7—Chula Vista. The species may have disappeared from southern California during the post-glacial Xerothermic period which brought hotter, drier conditions to the coastal strip.

in which the California taxa evolved. On this basis, records of fossil allies of the latter species are to be expected in the interior. A cone scale of a species allied to *P. sabiniana* occurs in the Miocene Anaverde flora of the western Mohave Desert (Axelrod, 1950). Its position 0.5 km west of the San Andreas fault is consistent with this thesis.

SUBSECT. CONTORTAE

Members of this alliance have been recorded in the late Eocene (38 Ma) Bull Run flora, northeastern Nevada (in Axelrod, 1968), the late Oligocene (26.5 Ma) Creede flora, Colorado (Axelrod, unpubl.), and the Early Miocene (21 Ma) Alvord Creek flora, southeastern Oregon (Axelrod, 1944). The first site is a rich montane conifer forest, the others are mixed conifer-hardwood forests. There is no evidence that *Contortae* were abundant in these floras. Their rise to prominence in the modern flora appears to be a later Cenozoic event, with rising mountains and spreading cold providing suitable environments for them, and with logging and fires, often set by man, aiding their rapid spread and crowding out of associated trees.

Pinus contorta var. *contorta* has a discontinuous distribution on the California coast from near Pt. Arena northward (Text-Fig. 21). This is probably a relict late Pleistocene occurrence, for the area has cool summers suited to its survival at the south. Its distribution is paralleled by *Picea sitchensis,* a species that ranged to Tomales Bay, 150 km farther south in the late Pleistocene (Mason, 1934). The var. *murrayana* of the Sierra-Cascade axis is discontinuous to the high mountains of southern California and Baja California (Text-Fig. 21). The latter sites are relict from the Early Quaternary (2 Ma), when mixed-conifer forest in interior southern California was fully 1,000 m lower in altitude (Axelrod, 1966b) and continuous with that in the Sierra Nevada. Later uplift of the Peninsular-Transverse ranges disrupted the earlier distribution of the mixed-conifer forest and accounts also for the disjunct occurrence of *P. contorta* var. *murrayana.*

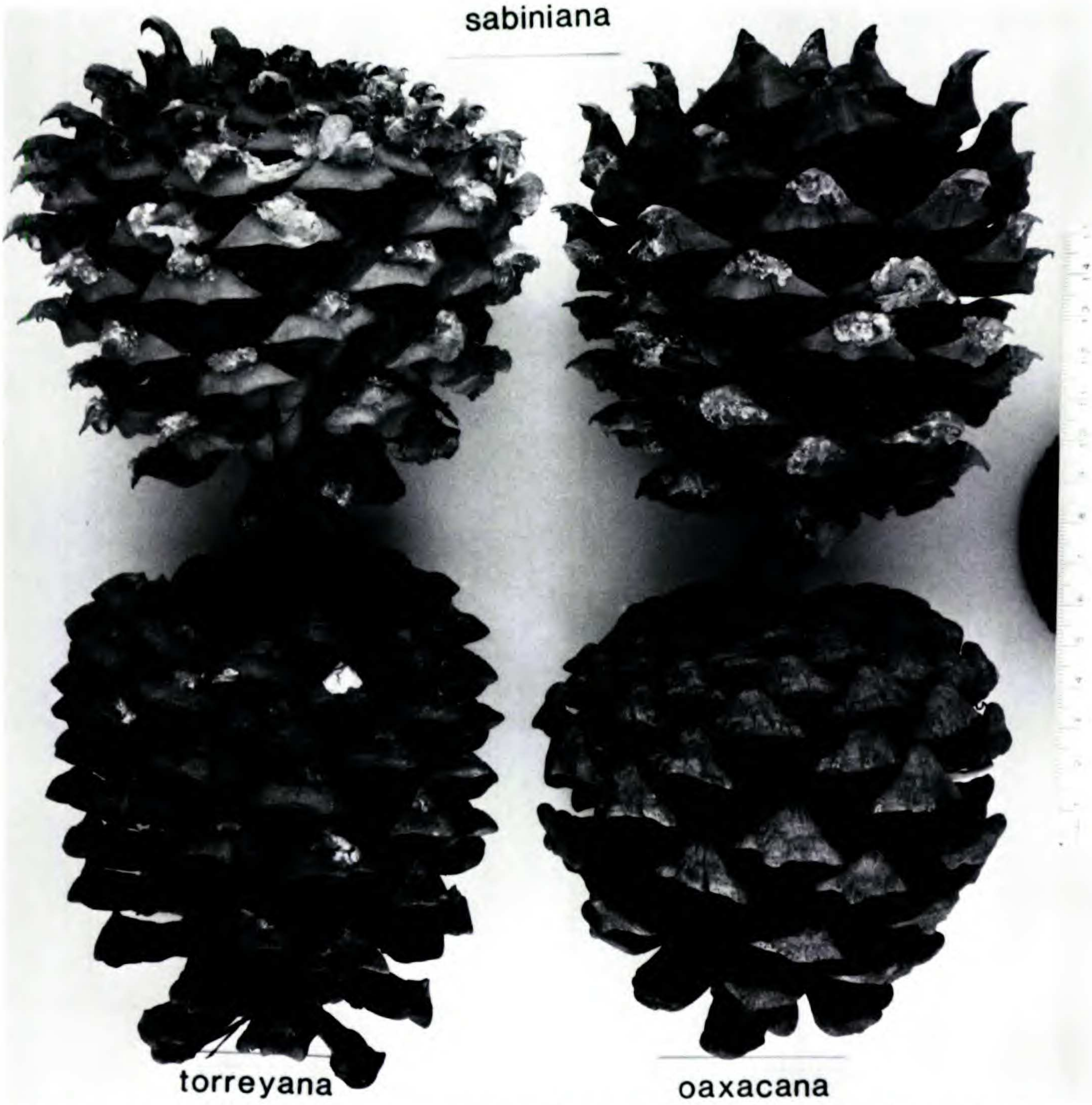
The isolated *P. clausa* of Florida and nearby Alabama may have been derived from *P. virginiana* in the later Tertiary as climate cooled and a population was isolated at the south. Confined to dry (sandy) sites, it either escaped or survived competition of taxa in the rich, mixed-mesophytic forest of the region during the climatic fluctuations of the Quaternary.

SUBSECT. OOCARPAE

Fossils of this group are presently known from California, Nevada, and Oregon in the west, and from Massachusetts in the east. Some of these are certainly extinct. *Pinus tiptoniana* Chaney & Axelrod (1959) from eastern Oregon appears allied to species like *P. patula* and *P. pringlei* as judged from its umbo relationships. *Pinus burtii* Miller (1978) from Martha's Vineyard, Massachusetts, is a large-coned species that may be distantly related to the *P. radiata* complex. This is suggested by the large, rounded apophyses, although the cone appears more nearly symmetrical. *Pinus burtii* provides a link with the upland flora of central Mexico where other members of the *Oocarpae* now occur. Continuity with the pines of Mexico is certainly old and probably is Late Eocene-Early Oligocene. Recall that the Late Eocene (35 Ma) Barilla flora of trans-Pecos Texas (Berry, 1919) represents a rich palm-laurel forest in this now semi-desert area. Furthermore, the Appalachians already supported an Eocene temperate deciduous forest as judged from the pollen record (Gray, 1960), and the inner lowlands of the Gulf Coast were covered with a rich, warm temperate forest with many taxa now in Mexico (Fredericksen, 1980, 1981). A warmer, milder climate is indicated also by the Miocene Legler flora (11 Ma) in the Cohansey Formation, New Jersey (Greller & Rachele, 1983). It has several genera (e.g., *Cyathea, Podocarpus, Engelhardtia*) now in the mountains of eastern Mexico, under wet, equable climate.

At present, numerous species and varieties of trees and shrubs are common to the temperate forest of the uplands of eastern Mexico and the eastern United States (Harshberger, 1911; Axelrod, 1939: 78; 1960: 267–268; Graham, 1973). A corridor via the Appalachians-Ozarks-trans-Pecos Texas and into Mexico in the Late Eocene-Early Oligocene may account for these ancient, surviving links, and suggests stasis for these taxa extends back fully 30–25 Ma. Elimination of species of present temperate Mexican occurrence from the eastern United States resulted from the trend to less equable climate later in the Cenozoic, and especially in the Pleistocene. It also eliminated many subtropical broadleaved evergreens, leaving the present impoverished deciduous hardwood forest with a few evergreen dicotyledons confined chiefly to the milder coastal strip, as exemplified by *Gordonia, Ilex, Magnolia, Persea,* and *Quercus* (*Q. virginiana, Q. laurifolia*).

Members of the *Oocarpae* now in California include three species in the coastal area (*P. remorata, P. radiata, P. muricata*) and one (*P. attenuata*) in the interior and in southwest Oregon (Vogl et al., 1977). The nearest affinities of *P. radiata* and *P. remorata* are with *P. oocarpa,* now in Mexico. *Pinus oocarpa* has cones very similar to those of *P. remorata* and to the small-coned *P. radiata* var. *cedrosensis* of Cedros Island and *P. radiata* var. *binata* of Guadalupe Island (Axelrod, 1980; Text-Fig. 22). Evidence suggests that the *Oocarpae* now in maritime California were displaced northward as terrain west of the San Andreas rift zone moved to its present area (Text-Fig. 23). This was from an earlier position that placed southern California at the latitude of Sonora, with the Cape Region of Baja California nestled near Cabo Corrientes, Jalisco (see Text-Fig. 12). The *P. radiata* populations on islands off Baja California (*P. radiata* vars. *cedrosensis* and *binata*) may be relicts of that distribution. In addition, a number of trees and shrubs associated with the *Oocarpae* in coastal southern California and northern Baja, California (e.g., near Eréndira) also appear to be remnants of that movement. These include narrow endemics that find their nearest allies in the mountains of Mex-

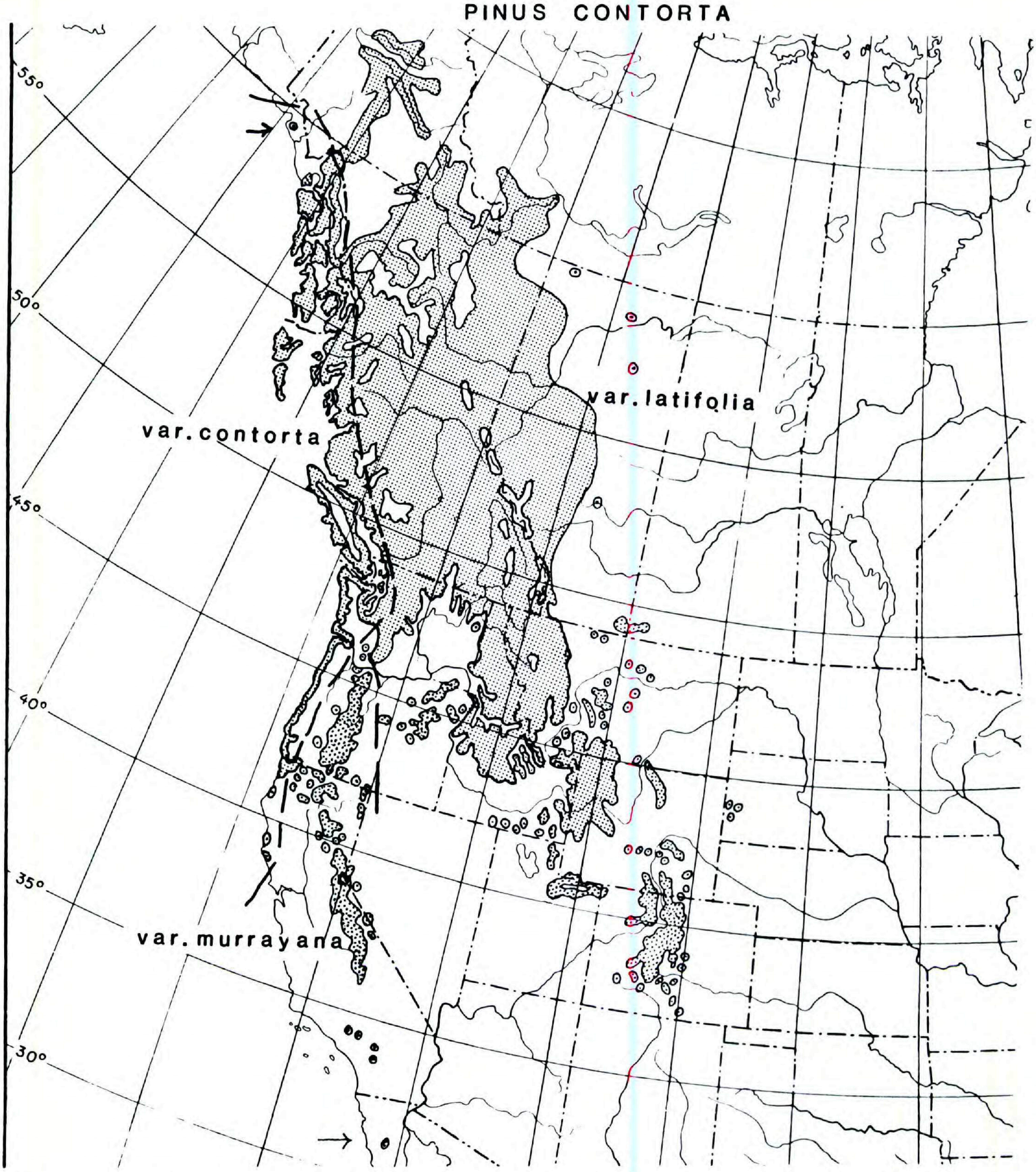


TEXT-FIGURE 20. Cones of *Pinus torreyana* are similar to those of *P. oaxacana.* In addition, both have long needles in 5s and large sheaths. The fossil forerunner of *torreyana* may have been was displaced northward by movement on the San Andreas fault system during the Miocene and later (see Text-Fig. 12).

ico where they are also associated with *Oocarpae.* Examples are in paired-species of *Arbutus, Ceanothus, Cercocarpus, Comarostaphylis, Myrica, Pinus, Prunus* (*Laurocerasus*), *Quercus,* and *Vaccinium* (Axelrod, 1967b).

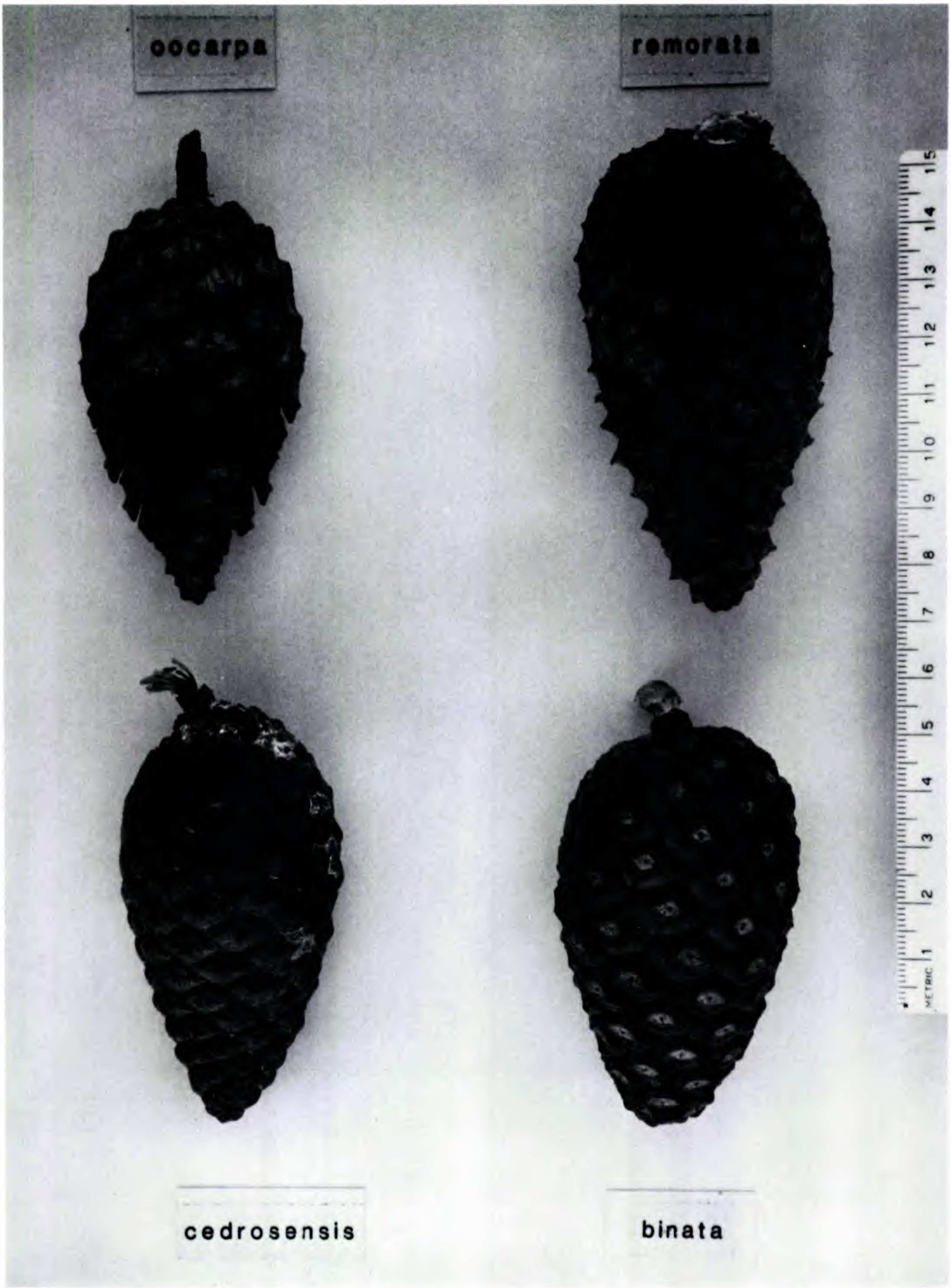
With respect to evolution of the *P. radiata* series, the var. *cedrosensis* appears to simulate the most ancient member of the alliance for its cones are very similar to those of *P. oocarpa.* A *P. radiata* var. *cedrosensis*-like population presumably gave rise to the Guadalupe Island *P. radiata* var. *binata.* The latter appears to have been ancestral to the California populations (Text-Fig. 24). Its cones range from those with apophyses scarcely developed (like *P. radiata* var. *cedrosensis* and *P. remorata*) to those that are inseparable from cones of the Monterey population. Similar variation occurs in cones recovered from the Pliocene San Diego Formation at Chula Vista, which places the insular *P. radiata* var. *binata* on the mainland (Axelrod & DeMéré, 1984).

As land area west of the San Andreas and allied rifts moved north, climate there was becoming progressively drier in summer in response to cold-water upwelling along the coast. As summer rains decreased further, and the mediterranean-type



TEXT-FIGURE 21. Distribution of three varieties of *Pinus contorta* today (map from Little, 1971). The southernmost sites for coastal *P. contorta* var. *contorta* evidently were attained in the Late Wisconsin. The occurrence of *P. contorta* var. *murrayana* in southern and Baja California apparently dates from the early Quaternary (2 Ma) when forest taxa lived about 1,000 m lower than they do today (Axelrod, 1966).

climate became more intense, cones of the three California populations evidently increased in size and also developed larger apophyses and seeds. The population at Monterey-Carmel has smaller cones than the stands 70 km northwest at Año Nuevo or 135 km southeast at Cambria (Text-Fig. 25). This apparently reflects survival of an older population in the cooler, foggier climate at Monterey. It results from the influence of the Monterey submarine canyon on local climate there, an area where two cypresses (*Cupressus macrocarpa, C. goveniana*) also have relict occurrences, as do a number of shrubs and forbs (Axelrod, 1982).

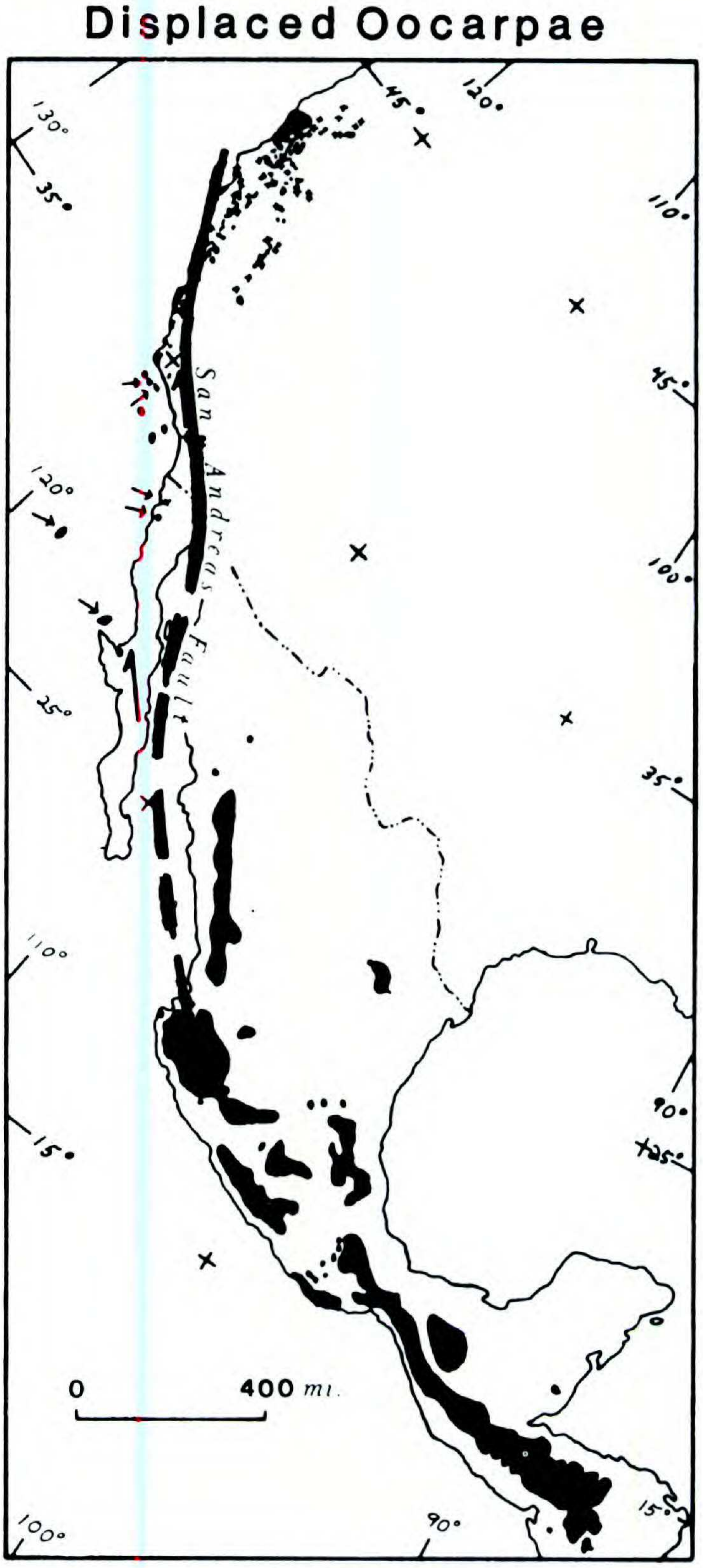


TEXT-FIGURE 22. Cones of four closely related pines of Subsect. *Oocarpae, P. oocarpa, P. remorata,* and *P. radiata* vars. *cedrosensis* and *binata.*

Pinus radiata, P. muricata, and *P. remorata* all had wider occurrences in coastal California in the Late Pleistocene (Axelrod, 1967a, 1967b). *Pinus radiata* evidently formed a nearly continuous forest from near Inverness, 60 km northwest of San Francisco (Axelrod, 1976a, 1980), to Chula Vista near San Diego (Text-Fig. 26), some 825 km southeast (Axelrod & DeMéré, 1984). The record of *P. muricata* is not so complete, but it certainly had a wider occurrence, for the northern population *P. muricata* var. *borealis* reached south at least to the Santa Barbara area. *Pinus remorata* also occurred more widely than at present. Restriction of these taxa to local areas today is chiefly the result of the warmer, drier, post-glacial climate, and especially that of the Xerothermic, which disrupted the more mesic forests. The present relict populations survive chiefly in areas of favorable, local climate where cold-water upwelling gives those areas a cooler climate with a high fog frequency. A similar relation exists at Eréndira, Baja California, where *P. remorata* and *P. muricata* occur in a semidesert climate bordering an ocean that is much colder and foggier in this local area (Axelrod, 1982).

The other member of the *Oocarpae* in California is *P. attenuata,* confined chiefly to interior regions, generally at the lower margin of mixed-conifer forest. It is most nearly allied to the Mexican *P. greggii, P. patula,* and *P. pringlei,* although the cones of *P. attenuata* are more strongly armed. The fossil *P. pretuberculata* may have spread northward from an ancestral, interior plexus and then been stranded in California as developing arid climate to the south disrupted its connection with the Mexican taxa (Axelrod, 1979). In this respect, the isolated *P. attenuata* population east of Ensenada has cones somewhat intermediate in shape to those of central Mexican species.

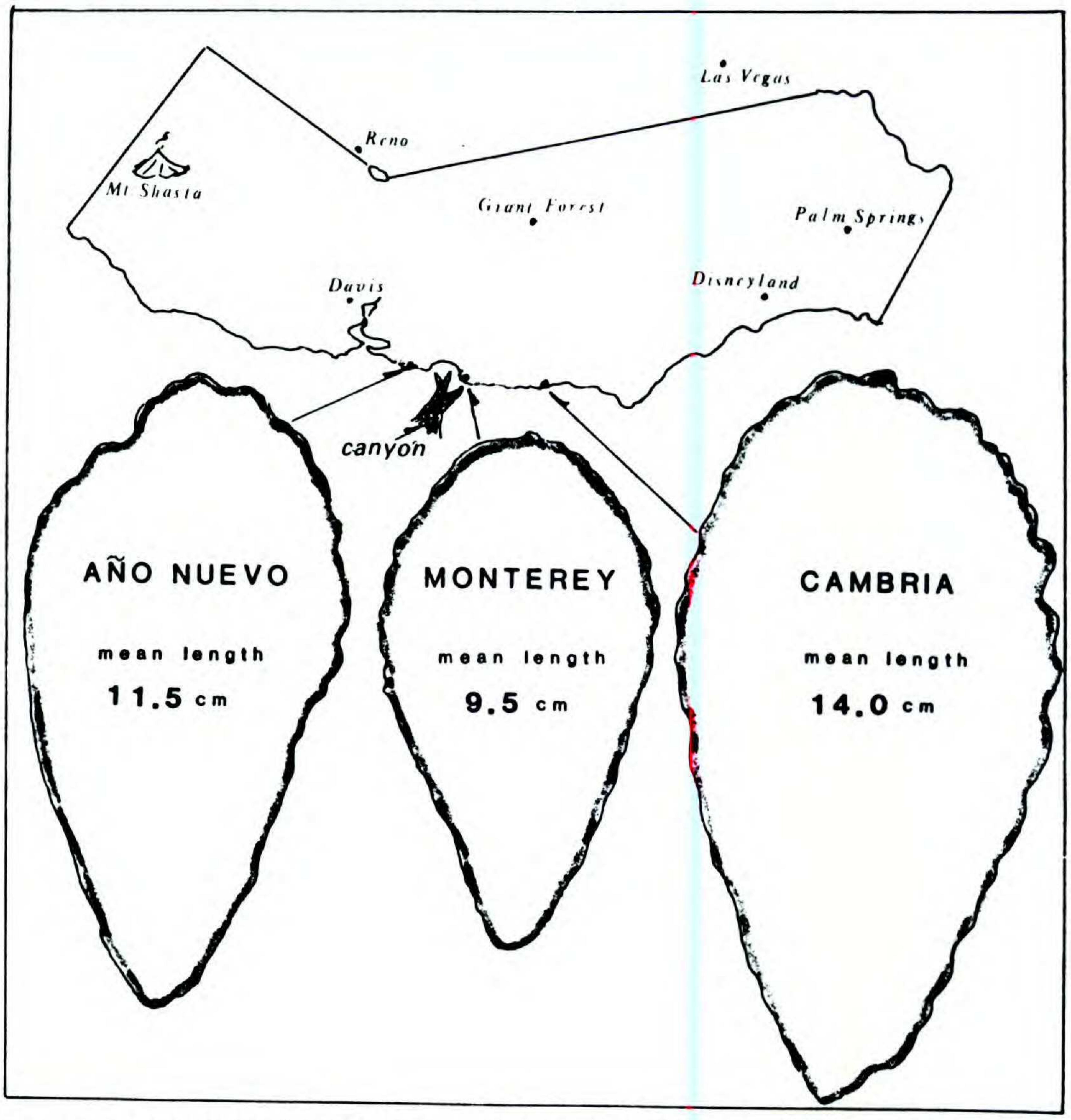
The fossil *P. pretuberculata,* which is very similar to cones of *P. attenuata,* was already in California in the Upper Miocene (12 Ma) Table Mountain flora (Condit, 1944). It is recorded from youngest Miocene rocks (5–6 Ma) in the Mount Eden flora of southern California (Axelrod, 1937) and the Verdi of western Nevada (Axelrod, 1958). *Pinus attenuata* is also in Early Pleistocene rocks at Signal Hill (Mason, 1932) and Seacliff (Axelrod, 1983), coastal southern California. At these latter sites, the cones probably were transported from the interior. This is likely because *P. at-*



TEXT-FIGURE 23. Distribution of species of *Oocarpae,* with four species each in California-Baja California (*P. attenuata, P. muricata, P. radiata, P. remorata*) and Mexico (*P. greggii, P. oocarpa, P. patula, P. pringleii*). (Map from Critchfield & Little, 1966.) The taxa in coastal California-Baja California evidently were displaced northward by movement on the San Andreas rift system (see Text-Fig. 12), as were other taxa whose nearest allies are now in Mexico (see text). Spreading desert climate further isolated these taxa.

TEXT-FIGURE 24. Variation in cones of *P. radiata* var. *binata* suggests that it may have been ancestral to the present California populations. This inference is consistent with the occurrence of Pliocene cones at Chula Vista, southern California, similar to those of var. *binata*. Increasing summer drought in California evidently resulted in the trend to larger cones and seeds.

tenuata occurs at these sites with closed-cone pines (*P. muricata, P. radiata*) that require humid, equable climate, whereas *P. attenuata* regularly inhabits drier sites away from the coastal lowlands, in more extreme climates of the interior. The species is restricted now to isolated stands in southern California, on the crest of the Santa Ana Mountains, and in the San Bernardino



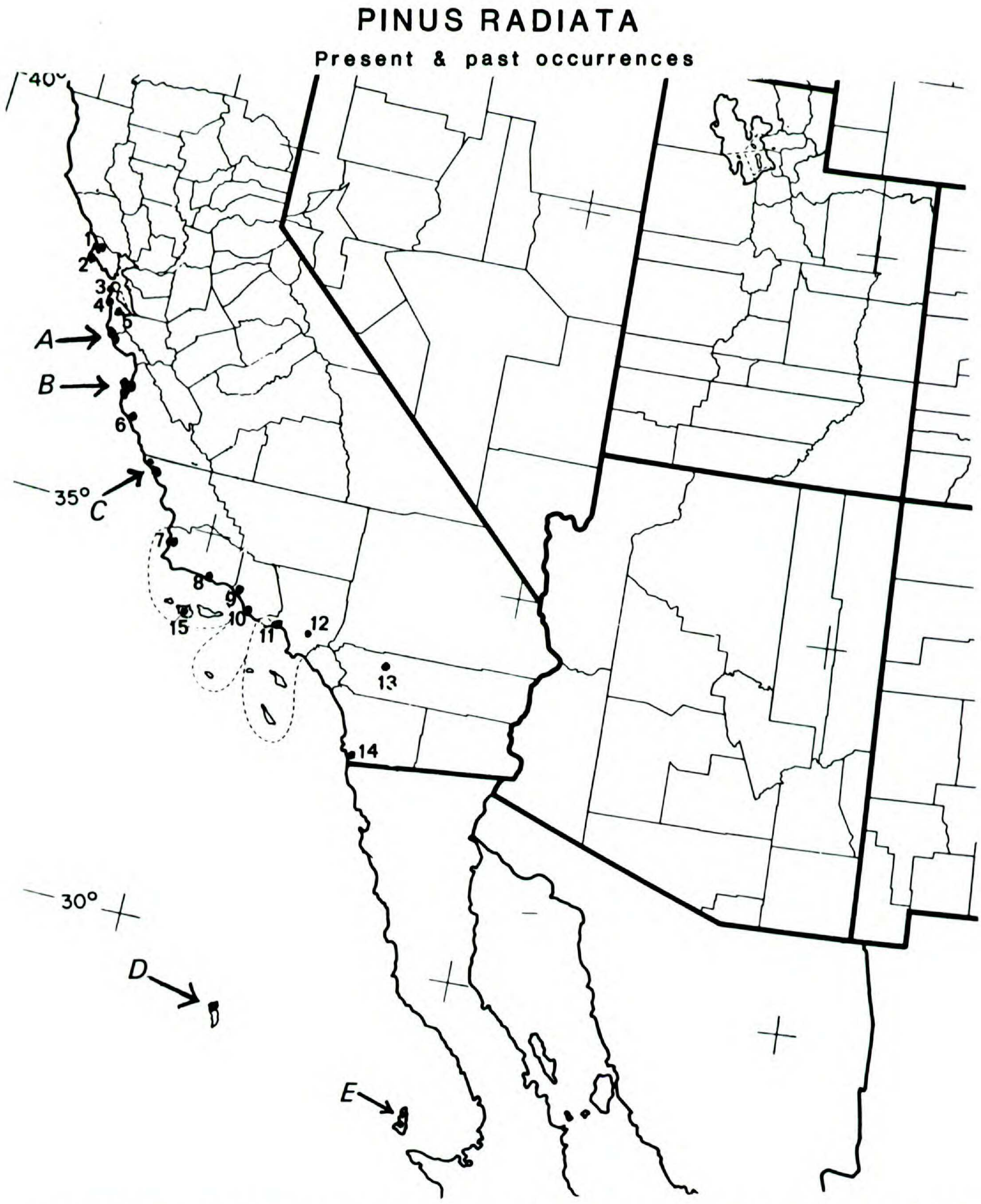
TEXT-FIGURE. 25. The California populations of *P. radiata* have larger cones and apophyses than do the Mexican populations from Cedros and Guadalupe islands. Although the larger cones appear to represent a response to increasing summer drought in California, note that the Monterey population has smaller cones than do populations at Año Nuevo and Cambria to the north and south. This reflects the position of the Monterey population opposite Monterey submarine canyon, where cold water upwelling makes the Monterey area the foggiest part of the coastal strip. Thus protected from spreading drought, the small-coned, probably ancestral, Monterey population has survived there with other relict endemics (from Axelrod, 1982).

Mountains. These local ocurrences, as well as the relict population east of Ensenada, may have resulted from restriction during the Xerothermic, when semi-desert taxa moved coastward from the interior and forests retreated upslope.

A unique Late Pleistocene occurrence is provided by a cone of *P. attenuata* recovered from an excavation at Oakland, on the east side of San Francisco Bay (Metcalf, 1923). Today the nearest stand is east of the Oakland Hills, some 12 km distant, where climate is hotter in summer and colder in winter. The pine evidently extended west to Oakland in a Late Pleistocene glacial age when sea level was about 100 m lower and the shoreline was fully 50 km (30 mi.) farther west (Helley & LaJoie, 1979). Climate was then more continental in the San Francisco Bay trough, which was dry land, as shown also by mammoth and other mammals recovered there during dredging. With the rise of sea level, and the return of milder, oceanic climate, the Oakland *P. attenuata* population disappeared, leaving survivors in the interior. A few interior species that still have rare populations in the Bay area probably are also relicts of the drier, Xerothermic climate (Axelrod, 1981).

LATE CENOZOIC EVOLUTION

Into the middle Tertiary many trees (probably most) of temperate regions had comparatively wide distributions that resulted from low environmental diversity. Climates were broadly zoned, they were highly equable, and more aseasonal in lower latitudes. Furthermore, terrain differences were not so marked as those of today.



TEXT-FIGURE 26. *Pinus radiata* occurs today at: A—Ano Nuevo, B—Monterey-Carmel, C—Cambria, D—Guadalupe I., and E—Cedros I. Fossil localities for Monterey pines occur at: 1—Tomales Bay, 2—Drakes Bay, 3—Thornton Beach, 4—Mussel Rock, 5—Spring Valley Lake, 6—Little Sur, 7—Pt. Sal, 8—Carpinteria, 9—Seacliff, 10—Pico, 11—Potrero Canyon, 12—Rancho La Brea, 13—Mount Eden, 14—Chula Vista, 15—Santa Rosa I. Disruption of the Late Pleistocene forest probably resulted from spreading Xerothermic climate that brought hotter, drier interior conditions to the coastal strip. The present relict stands are all confined to local areas of high fog frequency during summer.

High continuous ranges like the Sierra Nevada-Cascades or the Rocky Mountains, and high plateaus (Colorado Plateau, Mexican Plateau) had not yet come into existence. As regional topoclimatic differences developed later in the Cenozoic, the stage was set, especially in Mexico, for the rapid splitting of populations into new races, varieties, and probably some species.

Apart from geographic (spatial) and ecologic (edaphic) differences, isolation of populations may also result from seasonal climatic differences that determine times of major reproductive events (Stebbins, 1950: 208–209). This is seen notably in the co-occurrence at Monterey of *Pinus radiata* and *P. muricata,* which do not form hybrids because of fully two months difference in maturation of microsporangia. A similar separation is seen in the populations of *P. radiata* and *P. attenuata* at Swanton and Año Nuevo, north of Monterey. Differences in time of "flowering" that isolate populations may account for different populations (or varieties) of piñon (*P. cembroides*) recently described from the Southwest and Mexico. Most live under subhumid to marginally semiarid climates and are spread across 23° of latitude, or 2,800 km (1,775 mi.). Times of pollination vary greatly across this broad region depending on local climates (warmth), which are the result of recent tectonism that formed the ranges and basins in which these populations now occur. A similar explanation may also apply to *Pinus ponderosa,* which releases pollen at very different times of the year in British Columbia, Utah, California, and San Luis Potosí at its southern occurrence. These regional differences may have been a factor in the rise of varied races in these areas of very different rainfall and temperature regimes (adaptive subzones), and times of pollen shedding.

The closely similar species of *Strobi* that extend more or less continuously from the Canadian Rockies in British Columbia southward through the Sierra Madre Occidental into Guatemala, may also be considered in this context. There is a transition zone between *P. flexilis* and *P. strobiformis* and between *P. strobiformis* and *P. ayacahuite.* The shift from one species to the next occurs in areas of major topographic-climate change. These are along the Colorado-New Mexico border, and in the transition from central Arizona-New Mexico southward where climate rapidly becomes warmer (Axelrod & Raven, 1983), and in central Mexico, with warmer conditions farther south where *P. ayacahuite* occurs. The climatic differences, which determine time of pollen maturation, dispersal, and fertilization, have been intensified in the later Cenozoic. Natural hybrids of these species regularly occur in these transition zones.

Pines now in boreal regions and subalpine areas that form pure stands are subject to very low temperatures in winter. The most extreme are those in the area of *P. pumila* in northeast Siberia. Mean January temperature is −47.6°C (−52°F) at Verkhoyansk and −43.2°C (−45°F) at Yakutsk. Summers are sufficiently warm in these areas for boreal forest, with a mean July temperature of 16°C (60°F) at Verkhoyansk and 19°C (66°F) at Yakutsk. These extreme conditions developed recently, chiefly in the Quaternary. In the Middle Miocene (ca. 15 Ma) the area of northeast Siberia was covered with a rich conifer-deciduous hardwood forest much like that now on the middle mountain slopes from central Honshu to southern Hokkaido. This is apparent from the flora of Mammoth Mountain on the Aldan River (Dorofeev, 1969), about 200 km northeast of Yakutsk. It includes species of *Abies, Larix, Pinus, Acer, Betula, Broussonetia, Corylus, Cornus, Juglans, Morus, Padus, Prunus, Pterocarya, Salix,* and several others. Comparable Miocene floras are known also from Kamchatka (Menner, 1976), Sakhalin (Heer, 1878a, 1878b), Iceland (Heer, 1868), and Alaska (Heer, 1869). The shift to colder climate was largely post 5–6 Ma, as polar climates spread and mountains were elevated to alpine levels. This enabled subalpine and boreal conifers to form more continuous populations as hardwoods were eliminated by progressively increasing cold. During the later Tertiary, these northern coniferous populations adapted to more severe conditions by physiological shutdown (see discussion in Axelrod, 1983b: 126–128). This does not mean that pure conifer forests were not present until the later Tertiary—they were. The Eocene Upper Bull Run flora of northeastern Nevada is wholly dominated by conifers at seven sites distributed stratigraphically through fully 1,160 m (3,500 ft.). The conifers include species of *Abies, Larix, Picea, Pinus, Tsuga,* and *Chamaecyparis.* The only dicotyledons are a few shrubs distributed in *Crataegus, Holodiscus, Mahonia, Malus, Prunus, Ribes,* and *Salix.* This Upper Bull Run flora succeeded a mixed conifer-hardwood forest after 38 Ma as climates became colder (Fig. 2). If pure stands of pine (i.e., species of *Cembrae, Strobi, Balfourianae*) contributed to subalpine forests, they must have occupied slopes fully 500 m or more above the rich (15 taxa) montane conifer forest of the Bull Run basin.

A contributory role in the development of conifers, as well as vascular plants, has been played by mycorrhizal fungi, as discussed by Malloch et al. (1980). Pines have ectomycorrhizae, those in which the fungus surrounds the living cell of the root and does not penetrate it. The mycorrhizae extend out into the soil and serve to transfer nutrients from decaying litter into the plant from generally nutrient-poor soils. The mycobionts are very diverse in ectotropic forests, whereas the photobionts often form nearly pure, monotonous stands, as in the boreal and subalpine forests of colder regions (Malloch et al., 1980). Today, ectotropic forests like the boreal forest may commence on new sites with various dicotyledonous species, but the conifers become increasingly dominant. They may reach an equilibrium state that enables the best-adapted species to form forests of considerable stability (Meyer, 1973: 88). However, this is a new regional relationship, for pure conifer forests are not recorded as widespread, zonal vegetation types in the Tertiary. The available record in western North America indicates that they were restricted mostly to localized, higher and colder altitudes (see Axelrod, 1968; 1976a). Pure pine forests spread in response to increasing cold (*P. banksiana, P. contorta, P. cembra, P. pumila*), or drought (*P. cembroides, P. monophylla, P. edulis, P. ponderosa*), or to seasonality. As noted above, these are new environmental conditions in terms of forest history, whether in North America or Eurasia. Thus, the mycorrhizae have given Pinaceae, and *Pinus* in particular, an adaptive edge as environments have become more extreme, whether in cold regions, the seasonal tropics, or in edaphically unique areas (sandy sites, acid soils, etc.). The numerous pine species in Mexico occupy areas of seasonal climate and often poor soils. Many of these sites are on well-drained and effectively drier volcanic and carbonate rocks and hence are favorable sites for pines. These areas largely resulted from relatively recent volcanism or tectonism, which uplifted and exposed older rock units, often carbonates. With the presence of ectotrophic mycorrhizae in abundance, as well as seasonal climate affecting time of pollen shedding, fluctuating climate in the late Cenozoic, and more recently disturbance by man (fires, clearing), it is understandable that pines were able to form pure stands and many new races and varieties in the Mexican uplands and border areas.

The Quaternary changes noted above are further illuminated by a current paper by Critchfield (1984b) that considers the impact of Pleistocene climatic changes on the genetic structure and distribution of North American conifers, notably some species of *Abies, Picea,* and others. His interpretations are based on evidence from fossil pollen records, wood-rat middens, glacial and inter-glacial megafossil floras, and isoenzyme and terpene analyses of living conifers. In northern areas, the data provide evidence for population retreat during glacial times and their spread from refugia in post-glacial times. Over western areas, the record reveals the wider distribution of conifer species over lowlands presently desert and semidesert during the pluvials, as well as the occurrence of presently high montane conifers at altitudes fully 900–1,000 m lower. As Critchfield concluded, the most general effect has been the evolution and extinction of transitory races of boreal conifers, and, in some western conifers, the rise of longer-lived races through repeated cycles of isolation and hybridization. The influence of climatic fluctuations thus involved extinction of some species and races, the nearly complete loss of genetic variation in others, and occasional gene enrichment through hybridization and introgression.

FUTURE WORK

Discovery of new fossil ovulate pinaceous cones (*Pityostrobus, Pinus*) will no doubt further illuminate pine history. This will be particularly effective if large collections can be obtained, especially in older montane basins, or at higher latitudes, areas where Tertiary pines are more abundant. A most critical need, however, is the discovery of Tertiary floras in the Mexican uplands, a prime area of pine evolution. Comparisons of fossil taxa with species of modern subsections are necessary if we are to do more than merely describe new taxa.

Biochemical studies (isozymes, terpenes, DNA analysis) of modern species may provide evidence to estimate relative age of taxa. This would be of high interest for, in contrast to fossil species that have already developed their characteristics, the data may provide indications of the time of divergence of allied taxa. This could shed light on the age of presumably paired-taxa on different continents (*P. griffithii-P. monticola, P. cembra-P. albicaulis*) and in different parts of one continent (*P. strobus-monticola, P. edulis-monophylla*).

Continuing hybridization studies of modern species of the subsections may aid in further understanding species interrelationships.

CONCLUSIONS

The preceding review suggests that pines have been opportunistic throughout their history. They appear to have adapted early to generally stressful areas and probably originated there. Their evolutionary success probably was favored by their symbiotic relationship with ectotrophic mycorrhizae. This enabled them to inhabit drier sites, areas of seasonal rainfall, poor edaphic conditions (sand, laterite, podsol), and, late in their history, very cold regions. Pines responded rapidly on several occasions to increased topographic, climatic, and edaphic diversity by splitting into alliances ("subsections") of different adaptive mode. They have radiated into mountains in temperate and tropical regions, they inhabit dry areas at the lower limit of tree growth (*P. monophylla, P. ponderosa, P. sabiniana*), they have reached into extremely cold regions at timberline (*P. albicaulis, P. aristata*), at tree-line in boreal regions (*P. banksiana, P. pumila*), and others have entered seasonally dry tropical areas with leached soils (*P. cubensis, P. dalatensis*). More recently, pines have formed pure stands in colder (*P. banksiana*) and drier (*P. cembroides, P. ponderosa*) regions as older, richer forests and woodlands lost taxa and retreated to more favorable areas as climate changed. That pines are still opportunistic is evident in the uplands of Mexico for evolution is active there, as seen in the variation in *P. cembroides, P. montezumae, P. oocarpa, P. pseudostrobus,* and others. As on earlier occasions in pine history, Mexican pines recently responded to the rapid appearance of new environments—created there by volcanism, tectonism, new local climates, and fluctuating climate—to form new races and varieties by hybridization and introgression. Although pines are indeed ancient, they are highly successful. In terms of sheer numbers of individuals, there are more pines today than at any time in the past 140 million years, and they also wholly dominate vegetation over broad regions—a recent event.

PART 2. SYSTEMATICS

When George Englemann's *Revision of the Genus Pinus* was published in 1880, scarcely any fossil pines were then known from North America. A few had been described by Heer (1868–1882) from the high arctic and were assembled later in his six-volume classic, *Flora Fossilis Arctica.* Secured by various expeditions, the collections were small and inadequate, and the pines are represented chiefly by imprints of fragmentary needles, winged seeds, and a few broken cones. They are associated with taxa that contributed to deciduous-hardwood and conifer-hardwood forests of Paleocene, Eocene (Ellesmere I., Spitzbergen), and Miocene (Kamchatka, Sakhalin, Iceland, Alaska) age. In the volume describing the *Geological Exploration of the Western Territories,* Lesquereux (1878, 1883) reported on fossil floras from a number of localities in the western United States. Most of these represent vegetation of humid, warm temperate to subtropical environments, climates in which pines are largely absent. The early explorations of western Canada disclosed several small fossil floras in British Columbia and areas to the north (Dawson, 1883, 1890, 1891; Penhallow, 1908). They also contained scrappy remains of conifers, notably needles, winged seeds, and broken cones of pines and other conifers.

As more detailed geological studies of local areas proceeded during the decades following the 1920s, fossil floras were recovered from more numerous localities, and those from moderate altitudes often included remains of pines. Some of these, like the Copper Basin and Bull Run floras of northern Nevada, are in structural (fault) basins. Others, like the Creede of Colorado, the Hermosa of New Mexico, and the Thunder Mountain of Idaho, are preserved in sedimentary deposits that accumulated in the moats of large calderas that developed from collapse following explosive volcanism.

Although a century has elapsed since the early collections were made, our knowledge of pine history is still in a very preliminary state. This reflects the fact that there are relatively few good collections of fossil pines. Furthermore, since only a few investigators have been interested in the group, our understanding of pine history has been impeded further. In this review of previously-described as well as new Tertiary pines, attention is centered on the external form of cones pre-

TABLE 2. Tertiary ovuliferous *Pinus* cones with described internal structure.

Species	Structure	Occurrence and Age	Apparent Affinity
Pinus avonensis Miller (1969)	Cone	Near Avon, Montana, Oligocene	Subgenus *Pinus* (9 subsections)
Pinus arnoldii Miller (1973; Stockey, 1984)	Cone	Allenby Fm., B.C., Middle Eocene	*Sylvestres*
Pinus wolfei Miller (1974)	Cone	Cowlitz Fm., Wash., Late Eocene	*Contortae, Oocarpae, Sylvestres*
Pinus burtii Miller (1978)	Cone	Miocene Greensand, Martha's Vineyard, Miocene	*Oocarpae*
Pinus buchananii Underwood & Miller (1980)	Cone	Twin Bridges Fm., Wash., Oligocene	*Australes, Ponderosae*
Pinus escalentensis Banks et al., 1981	Cone	Escalente Fm., B.C., Oligocene	Sect. *Pinus* (6 subsections)
Pinus driftwoodensis Stockey (1983)		Driftwood Creek Beds, B.C., Middle Eocene	*Australes*
Pinus princetonensis Stockey (1984)	Cone	Allenby Fm., B.C., Middle Eocene	*Sylvestres*
Pinus similkameenensis Miller (1973)	Fascicle, 5s	Similkameen beds, B.C., Middle Eocene	*Strobus*
Pinus similkameenensis Miller (1973), Stockey (1984)	Wood	Similkameen beds, B.C., Middle Eocene	*Parrya*
Pinus allisonii Stockey (1984)	Fascicle, 2s	Allenby Fm., B.C., Middle Eocene	*Sylvestres*
Pinus andersonii Stockey (1984)	Fascicle, 3s	Allenby Fm., B.C., Middle Eocene	*Ponderosae*

served as imprints in fine-grained sedimentary rocks because the external characteristics of fossil cones are similar to living pines. Less emphasis is placed on isolated winged seeds and fascicles of needles because most cannot readily be assigned to species groups.

As discussed by Miller (1976), and Banks et al. (1981), cones of *Pinus* have four main features. Species of *Pityostrobus* may possess some, but not all of these: 1) ovuliferous scales inflated at apex, 2) vascular supply to bract-scale complex leaves axial cylinder as a single unit, 3) resin canals in the base of the scale are abaxial to the scale trace, and 4) the vascular bundles in the distal part of the scale are rounded on their adaxial side (Text-Fig. 1). While these differences may separate most Cretaceous and some Paleogene cones of *Pityostrobus* from those of *Pinus, Pityostrobus* cones certainly are pinaceous (Miller, 1976, table 2). Since fossil ovulate cones acknowledged to represent *Pinus* were already present in the Early Cretaceous (ca. 120–125 Ma) (Alvin, 1960), *Pityostrobus* species apparently represent surviving members of an older plexus from which *Pinus* had diverged by the latest Jurassic. Inasmuch as *Pityostrobus* has been recorded only once in the Paleocene (Miller, 1977b), it presumably largely became extinct in the Cretaceous-Tertiary transition, and was replaced by *Pinus*.

Studies of the internal structure of permineralized *Pinus* cones from older Tertiary rocks have not greatly clarified their relationships within the subsections (Table 2). Most of the described species have been compared with one or two subsections, yet cones of species in these alliances may differ considerably in external features (form; apophyses; umbo-mucro position, etc.). The diversity of cone types within these groups, as well as the megafossil record of external impressions, implies that a number of species in the subsections were already in existence in the Eocene (see below). One of the problems raised by studies of internal structure of fossil cones is that the external form of the cones and its features (apophyses, umbo-mucro) are not always available for analysis. Some described fossil cones are so incomplete, owing to erosion or decomposition prior to burial, that their external characteristics have been erased (e.g., *P. wolfeii, P. avonensis*), and the form of others, if preserved, was not illustrated or described prior to sectioning.

In view of the preliminary stage in our knowledge of American Tertiary pines, it is desirable to clarify the approach to systematics followed here. Since most fossil pine taxa are based on disassociated structures (cones, needles, winged seeds) at a given locality, these are grouped into species that appear to represent one taxon. In this way, a plethora of names that might otherwise be used is eliminated, and some semblance of biotic relationship can be suggested. For example, a cone of *Pinus* in the Late Eocene Bull Run flora is allied to *P. contorta.* Also in the flora are winged seeds that fall within the range of variation shown by that alliance. Seeds similar to those produced by *P. contorta* are in the Creede flora, Colorado. All this material is referred to the previously-described *P. alvordensis* Axelrod, which is a winged seed of the *P. contorta* alliance. It is granted that the fossils from these sites may represent different species of Subsect. *Contortae.* However, at this stage in our understanding of pine history, and in view of the limited sample, it seems best to group them into one fossil taxon, for the fossils can scarcely be separated taxonomically. A second example is provided by *Pinus crossii* Knowlton, based on fascicles of 5s in the Creede flora, Colorado. My large collections from 15 sites in the Creede Formation show that short needles in 5s are abundant at most sites. There are fossil cones and winged seeds in the flora similar to those produced by the living *P. aristata,* a species that has short needles in 5s. Rather than describe the cones and winged seeds as two additional species in the Creede flora, all of this material is referred to *Pinus crossii,* a species allied to *P. aristata.*

Identification of the fossils in this report has been based chiefly on comparisons with the large collection of modern pine material at the Institute of Forest Genetics, Placerville, California. This has made it possible to suggest relationships between the fossils and modern taxa, and hence to assign the fossils to subsections. It is emphasized that comparison of a fossil pine with a modern species does not mean that the living taxon has persisted unchanged from the Eocene or Oligocene down to the present. The comparison simply means that, as judged from what actually is available, a particular living species is most nearly related to the fossil pine which is given a separate name.

In the following discussion of some Tertiary pines, emphasis is on the imprints of fossil cones, for this is their usual mode of occurrence. Analysis of their modern relationships is aided by reference to the umbo-mucro features of the cone scale presented by Klaus (1980). Furthermore, appraisal of the affinities of cone imprints commonly is aided by making latex casts of the mold. In addition, the relationships of cones may be clarified by associated fascicles and winged seeds.

The Little and Critchfield (1969) system of classification followed here divides the genus into three subgenera, four sections, and 15 subsections (Table 2). The distribution of the modern species is well illustrated by Critchfield and Little (1966).

SUBGENUS STROBUS

SECT. STROBUS

Subsect. *Strobi*

This subsection includes six American and eight Eurasian species that occur chiefly in relatively mesic, mixed-conifer and conifer-hardwood forests. The close similarity between the American *P. monticola-strobus* and the Eurasian *P. peuce-parviflora-griffithii* pines is noteworthy. Future studies of their seed protein composition may indicate the times of separation of these allied species on each continent, and those that are now on separate land areas.

Although several species of Subsect. *Strobi* are on each continent today, there is no clear evidence that presently American species were represented earlier by similar species in Eurasia, or vice versa. The report that *Pinus monticola* var. *fossilis* (Sukachev, 1910) from the Pliocene of Siberia is similar to the present American *P. monticola* (Mirov, 1967: 56; Wolfe & Leopold, 1967: 199) is incorrect. The illustration shows that the cone differs from those of *P. monticola* in being more robust, is not so slender when closed (in water), and the cone scales are larger and thicker than those of *P. monticola.* The fossil is more nearly allied to present Asian species, notably *P. armandii* Franch. of central China. A similar, but more complete, cone of *P. itelmenorum* is in the Mammoth Mountain flora on the Aldan River (Dorofeev, 1969). Its more massive size and broader, thicker scales show that it is allied to *P. armandii* and its relatives, not to *P. monticola.*

Pinus anthrarivus Axelrod, sp. nov. TYPE: U.S.A. Idaho: Coal Creek. U.C. Mus. Pal., holotype 7165, paratypes 7166–69, 7218–20. Figures 1–5.

Needles in 5s, 4–6 cm long, very slender, averaging 0.5 mm broad; tips very acute; sheath deciduous. Winged seeds 1.5–2.5 cm long, seed ovate to oval, rounded distally, apex rounded to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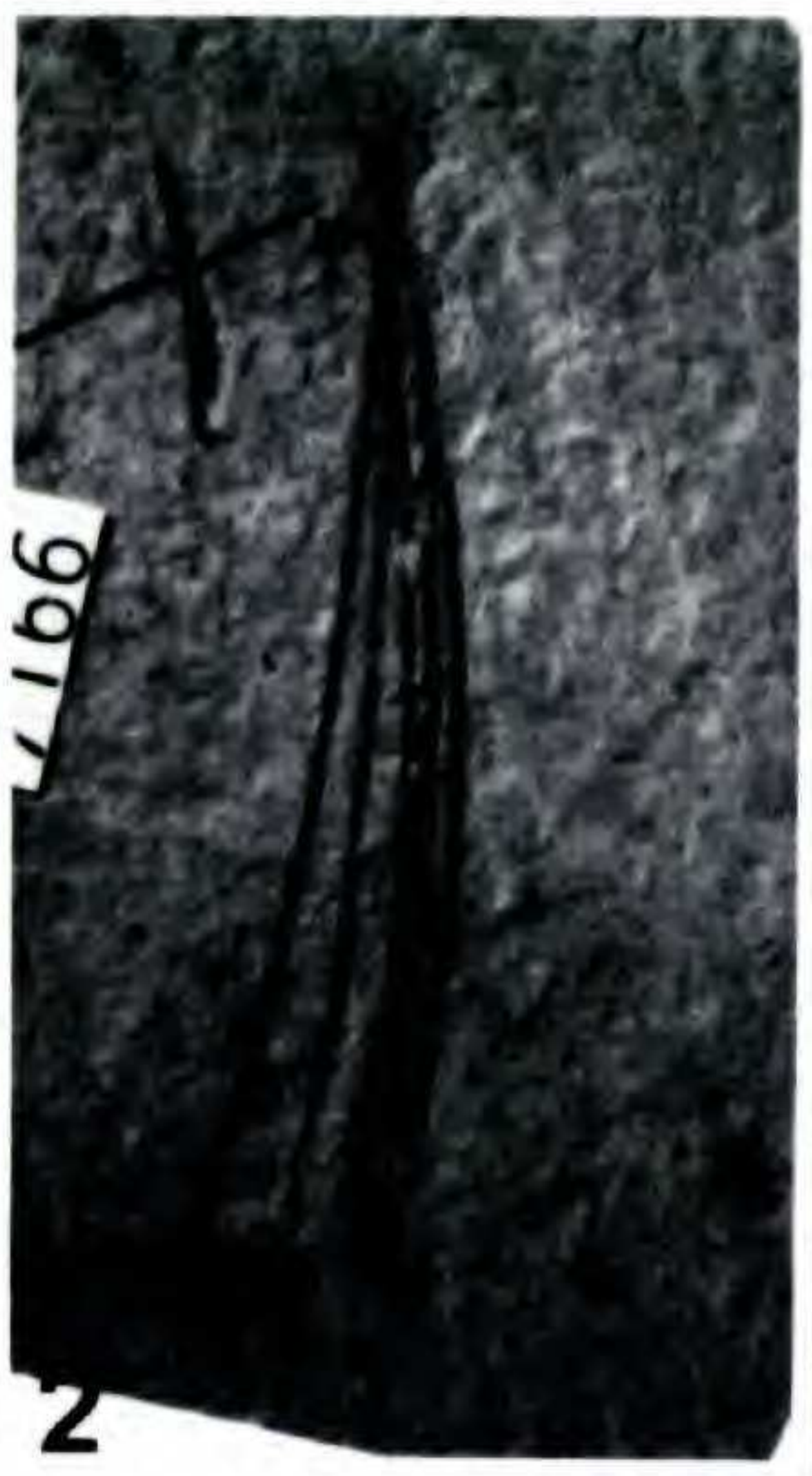
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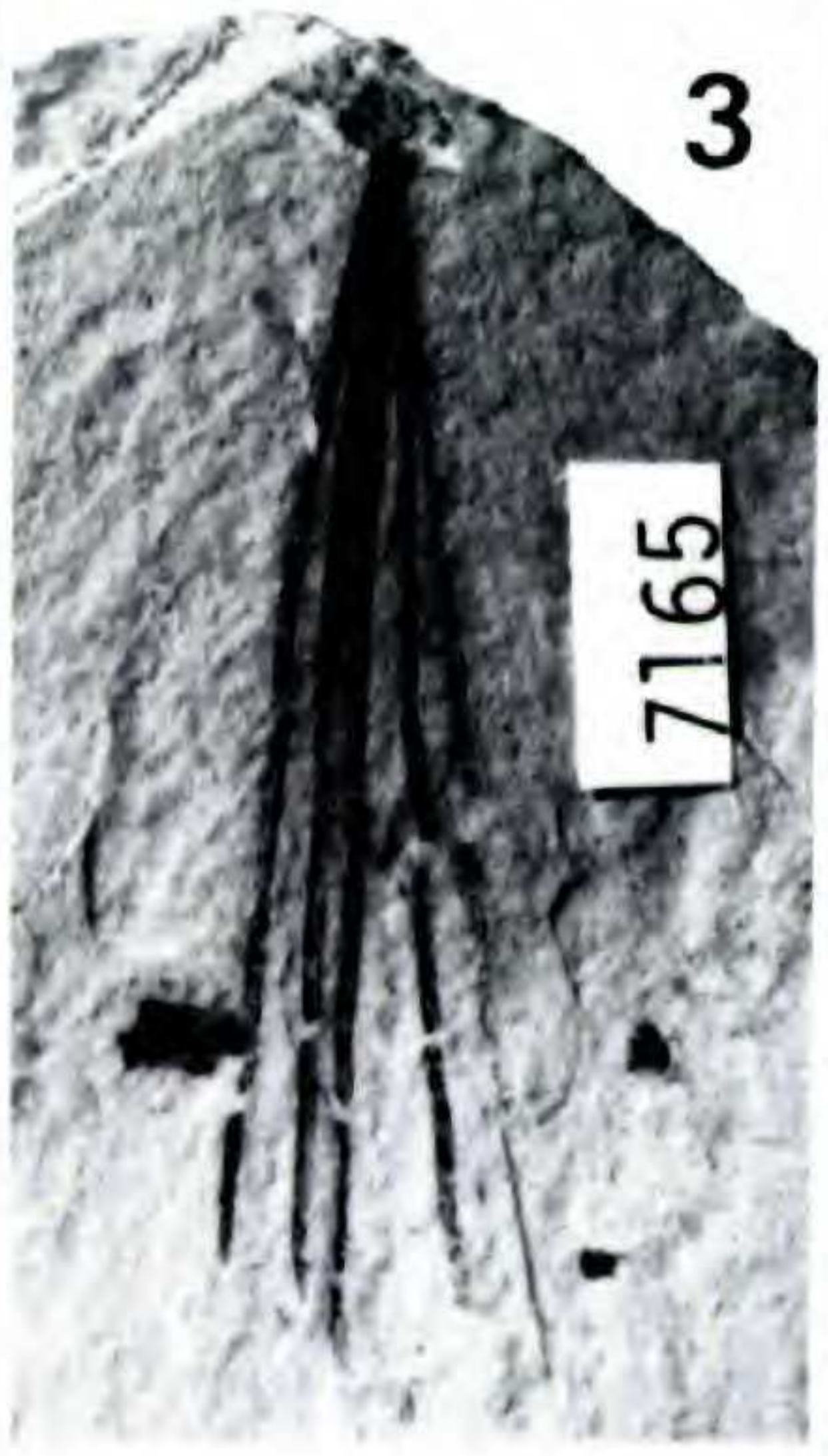
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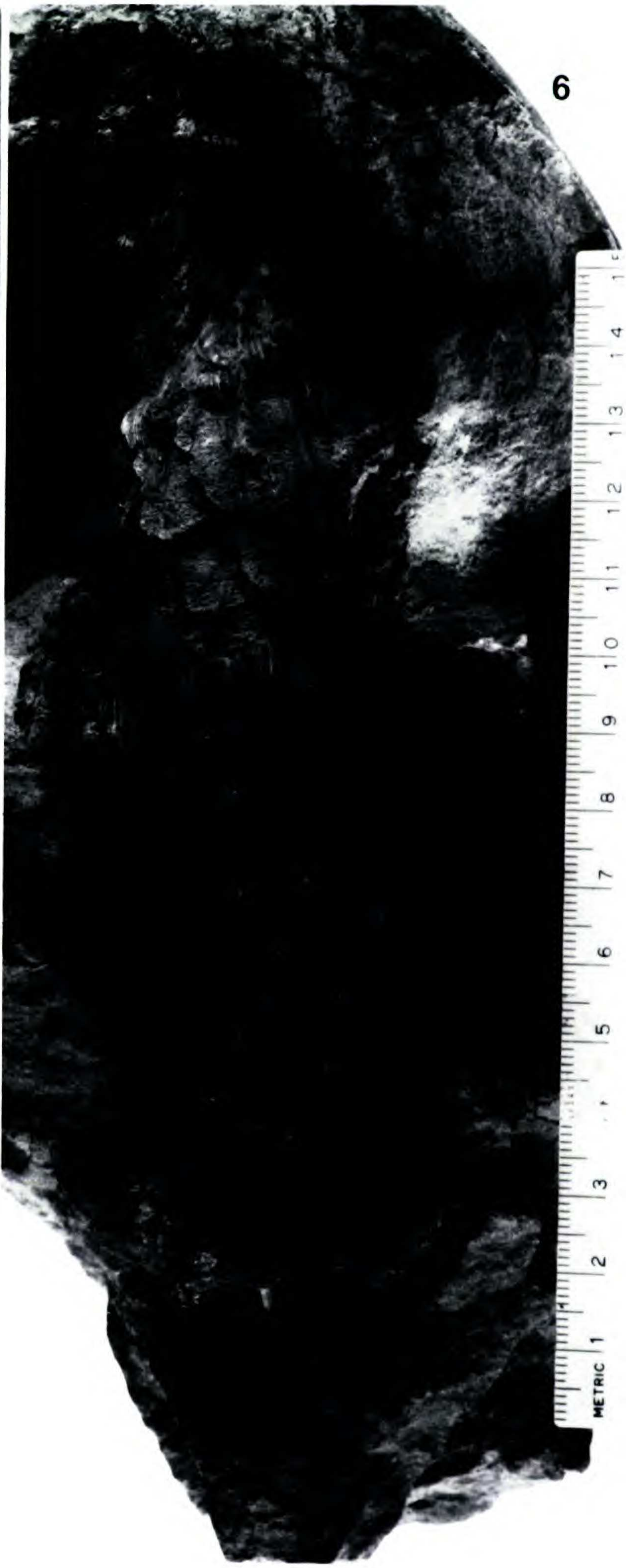
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blunt, wing widest near middle, distal end broadly rounded.

Discussion. The scores of fascicles in the Coal Creek flora with slender needles at first suggested relationship with *P. strobus,* rather than *P. monticola,* which has thicker needles. However, the winged seeds differ markedly from the slender wings with acute tips produced by those species. In general shape they are more nearly allied to species of *Groupo Ayacahuite* (Martinez, 1948), and especially to the seeds of *P. ayacahuite* var. *veitchii* Shaw. *Pinus anthrarivus* thus appears to be an ancient member of Subsect. *Strobi,* one showing relationship to present Mexican species of the *ayacahuite* complex.

A radiometric date indicates that the pine and associated flora is 29 Ma old, or Late Oligocene.

Pinus delmarensis Axelrod, sp. nov. TYPE: U.S.A. California: Del Mar. U.C. Mus. Pal., holotype 7170. Figure 6.

Cone closed owing to immersion in water; cone long-cylindrical; 26 cm long (estim.), 6 cm broad; cone scales thin, 3+ cm wide in middle of cone, flat to broadly concave, no evidence of pronounced reflexing; scales apparently with terminal umbos.

Discussion. This cone from the Del Mar Formation, a few miles north of San Diego, is associated with sediments that yield both a molluscan fauna (Hanna, 1926) and vertebrate fauna (Golz, 1976) of Middle Eocene age, approximately 46 Ma old.

The cone is so similar to those of *P. lambertiana* there is no ready basis for separating them. In view of the fragmentary nature and rarity of all presently-known specimens of this alliance, it seems best to tentatively consider that the species is different than *P. prelambertiana* Axelrod from the Late Tertiary. The record suggests that *P. delmarensis* may have been separated geographically from a complex that included forerunners of *P. strobiformis* Engelm. and *P. ayacahuite* Ehrenberg as California west of the San Adreas shifted north following the early Miocene.

The presence of higher relief in the region to the east is indicated by coarse conglomerates in the associated section and by the spore-pollen flora (Frederiksen et al., 1983). In particular, the presence of pine pollen allied to the *Ponderosae* and *Strobi* groups indicates that terrain in the interior probably was near 1,300–1,500 mm, whereas the coastal strip was covered with a dry tropical flora.

Pinus florissantii Lesquereux, Rept. U.S. Geol. Surv. Terr 8: 138, pl. 21, fig. 13, 1883. Florissant, Colorado. Princeton Univ. Paleobot. Coll. holotype 144. Figures 8, 9.

Pinus florissantii Lesquereux. MacGinitie, Carnegie Inst. Wash. Publ. 599: 84, pl. 19, fig. 2, 1953.
Pinus similis Knowlton, U.S. Geol. Surv. Prof. Paper 131-G, p. 186, pl. 41, figs. 12, 13, 1923.
Pinus wheeleri Cockerell. MacGinitie, ibid., p. 85, pl. 18, fig. 11 only, 1953.
Pinus leaves, MacGinitie, ibid., pl. 18, fig. 3, 1953.

Pinus similis Knowlton was based on two fascicles of four needles in the Creede flora. Many additional fascicles have now been collected, and it is evident that most are in 5s, but some are in 4s and, more rarely, in 3s. The last are probably the result of needle loss during ageing or transport. The suite of *P. similis* foliage from Creede is similar to that produced by the modern *P. flexilis* James, and is therefore placed in synonymy under *P. florissantii* Lesquereux, based on a cone similar to those produced by *flexilis* today.

Supplementary description. Fascicles mostly in 5s, some in 4s; needles 4.0–5.2 cm long, 1.0 mm wide, stout and mostly curved; margins entire, prominent stomatal bands; tip acute; sheath absent, the proximal end forming a rounded (globose) area.

Discussion. Knowlton made no suggestion as to the identity of the Creede foliage referred here to *P. florissantii.* Comparison with western members of the *Strobi* shows that it is most similar to foliage of *P. flexilis* James; fascicles of *P. monticola* are generally not so robust. *Pinus flexilis* is a regular member of the mixed-conifer forest of the central and northern Rocky Mountains. It is discontinuous across the central Great Basin to the east slope of the central and southern Sierra

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FIGURES 1–7.—1–5. *Pinus anthrarivus* Axelrod, sp. nov. Coal Creek, Idaho. U.C. Mus. Pal., holotype 7167, paratypes 7165, 7166 (needles), 7168, 7169 (seeds). Late Oligocene, 27 Ma.—6. *Pinus delmarensis* Axelrod, sp. nov. Del Mar Formation, California. U.C. Mus. Pal., holotype 7170. Middle Eocene, 48 Ma.—7. *Pinus prelambertiana* Axelrod. Vedder Sandstone, California. U.C. Mus. Pal., hypotype 7171. Lower Miocene, 23 Ma.


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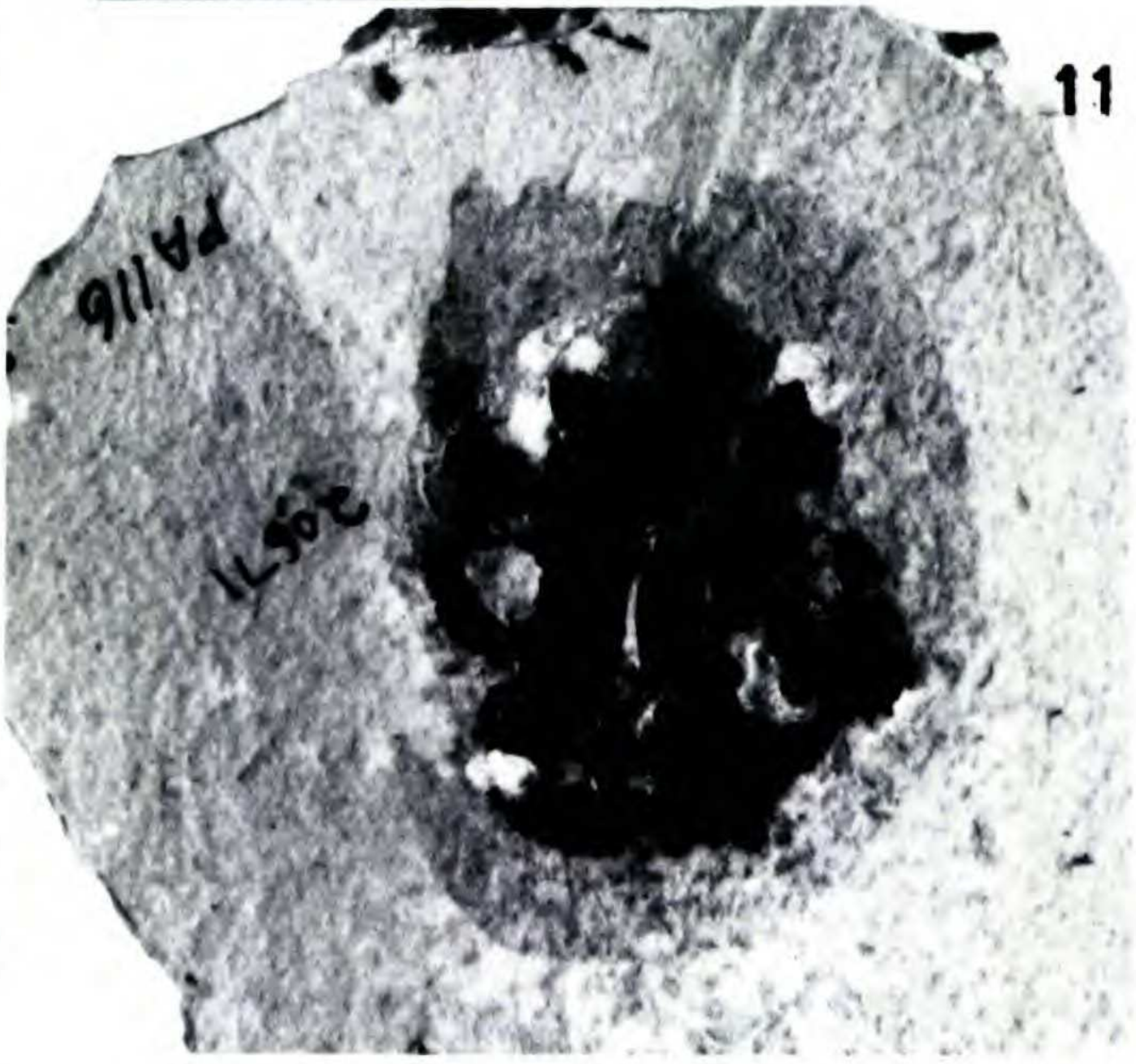

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Nevada, ranging southward in the Peninsular Ranges to the Santa Rosa Mountains, southern California.

The Florissant flora is well dated at 34 Ma, or earliest Oligocene (Epis & Chapin, 1975: 48).

Occurrence. Florissant, Colorado: U.C. Mus. Pal., hypotypes 3727, 3775; Creede, Colorado: U.C. Mus. Pal., hypotype 7214, homeotypes 7212, 7213.

Pinus prelambertiana Axelrod, Carnegie Inst. Wash. Publ. 412: 71, pl. 6, fig. 1, 1930. Santa Clara, California. U.C. Mus. Pal., holotype 309. Figure 7.

Pinus prelambertiana Axelrod, Univ. Calif. Publ. Geol. Sci. 24: 127, pl. 18, figs. 7–10, 1958.

The figured cone is from the Lower Miocene Vedder Sandstone at Pyramid Hill, northeast of Bakersfield, California. Vedder Sandstone is in the *Turritella inezana* zone and in the microfossil Zemorrian Stage, both of earliest Miocene age, 25–26 Ma (Turner, 1970).

Discussion. The cone is similar to those produced by *P. lambertiana* Douglas. The record indicates that in the Sierra Nevada to the east, climate was sufficiently moist and cool to support conifers. With ample summer rain and a more equable climate, the forest no doubt occurred at a lower altitude than the modern forest where *P. lambertiana* is confined now to altitudes above 1,300–1,500 mm.

Occurrence. Verdi, Nevada: U.C. Mus. Pal., hypotypes 1976–1978; Vedder Sandstone, California: U.C. Mus. Pal., hypotype 7171, homeotype 7172.

SECT. PARRYA

Subsect. *Cembroides*

Of the eight species of nut pine, four are in the United States—*P. monophylla* Torr. & Fremont, *P. edulis* Engelm., and with *P. quadrifolia* Parl. and *P. cembroides* Zucc., ranging into Mexico. Four piñons are confined to Mexico, *P. culminicola* Andres. & Bearman, *P. maximartinezii* Rzed., *P. pinceana* Gord., and *P. nelsonii* (Shaw). Several varieties of *P. cembroides* have been recognized in recent years (Bailey, 1979, 1983 gives references). These appear to be geographic races of relatively recent, probably Quaternary, origin.

The *P. cembroides* population isolated in the mountains of the Cape Region, Baja California, named *P. cembroides* var. *lagunae* Robert-Passini (1981), poses an interesting problem. The Cape Region separated from the mainland of Jalisco by northward movement of the San Andreas and allied rifts and later spreading along the mid-ocean rise, which opened the Gulf of California. This raises the question as to whether *a*) there are relict stands of the Cape piñon in the Sierra Madre Occidental masquerading as *P. cembroides*, or whether *b*) the Cape population was on the mainland and became extinct here, or *c*) whether the pine originated in the Cape Region from a *cembroides* population that was isolated there as the Cape Region separated from the mainland.

Piñons do not intercross with other members of the genus (Mirov, 1967: 334), although pines of other subsections may do so. This implies that *Cembroides* are ancient, consistent with the fossil record, which shows that piñon was already present in the Middle Eocene (46 Ma).

Pinus ballii Brown, U.S. Geol. Surv. Prof. Paper 185: 53, pl. 8, fig. 5, 1934. TYPE: U.S.A. Colorado: Green River. U.C. Mus. Pal., holotype 1927–20688. Figures 10, 11.

Pinus ballii Brown. MacGinitie, Univ. Calif. Publ. Geol. Sci. 83: 91, pl. 25, fig. 2, 1969.

A 3-needled fascicle with deciduous sheath (Fig. 10) and an impression of a cone (Fig. 11) rep-

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FIGURES 8–18.—8. *Pinus florissantii* Lesquereux. Florissant, Colorado. Princeton Univ., holotype 144. Basal Oligocene, 34 Ma. (Previously figured by Lesquereux [1883] and MacGinitie [1953].)—9. *Pinus florissantii* Lesquereux. Creede, Colorado. U.C. Mus. Pal., hypotype. Late Oligocene, 26.5 Ma.—10. *Pinus ballii* Brown. Green River, Colorado. U.C. Mus. Pal., holotype 1927 (20688). Middle Eocene, 46–47 Ma. (From Brown, 1934.)—11. *Pinus ballii* Brown. Green River, Colorado. U.C. Mus. Pal., hypotype 20671. Middle Eocene, 46–47 Ma. (From MacGinitie, 1969.)—12. *Pinus sanjuanensis* Axelrod, sp. nov. Creede, Colorado. Univ. Colorado Mus., holotype 19701. Late Oligocene, 26.5 Ma.—13–16. *Pinus sanjuanensis* Axelrod, sp. nov. Creede, Colorado. U.C. Mus. Pal., paratypes 7239–7241, 7243. Late Oligocene, 26.5 Ma.—17. *Pinus lindgrenii* Knowlton. Chalk Hills, Idaho. Jurupa Cultural Center, California, hypotype 11205. Late Miocene, 5–6 Ma.—18. *Pinus lindgrenii* Knowlton. Chalk Hills, Idaho. U.S. Nat. Mus., holotype 8179. Late Miocene, 5–6 Ma. (From Knowlton, 1901.)

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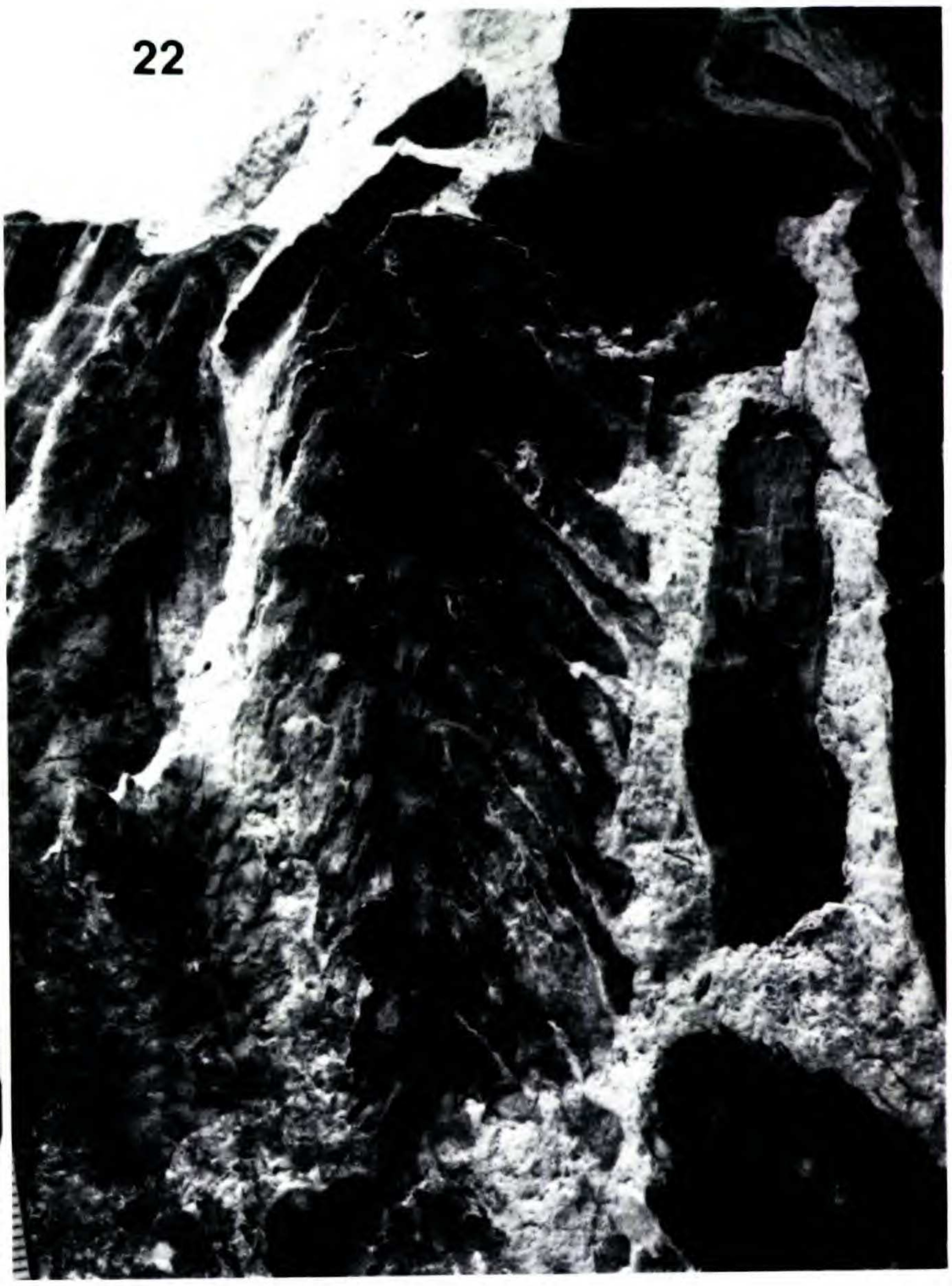

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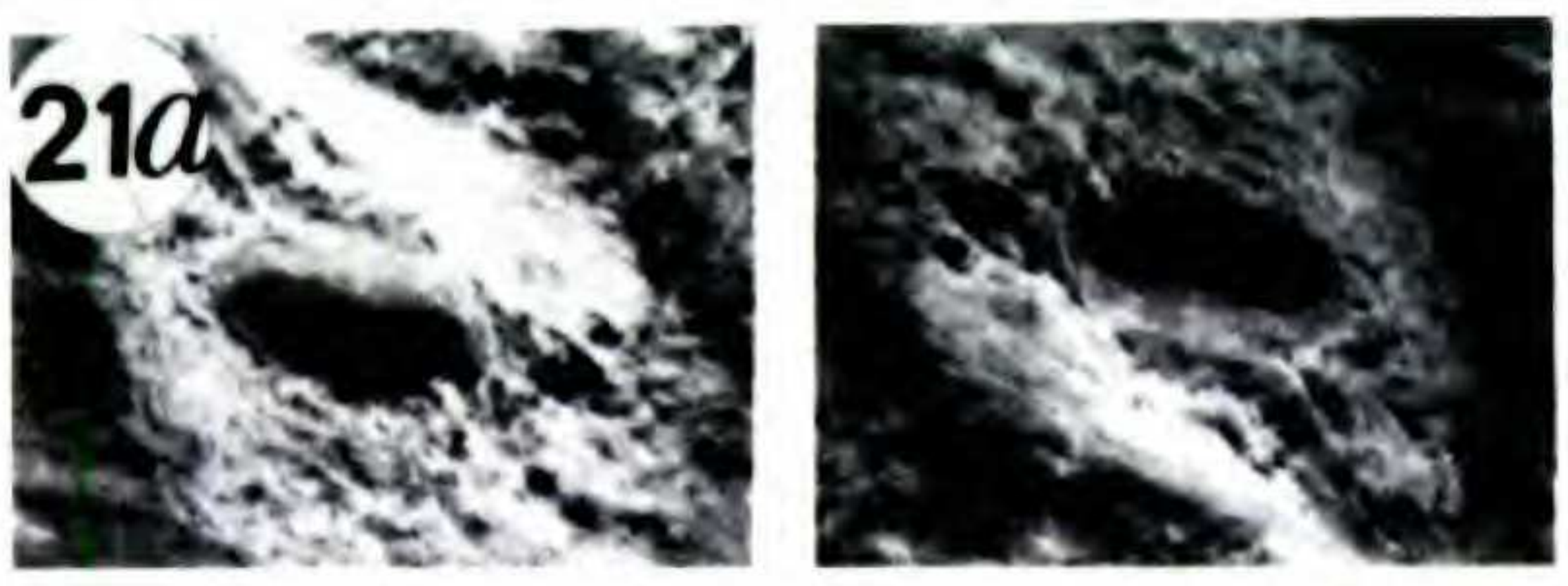

resent a piñon in the Middle Eocene Green River flora, dated at 46–47 Ma.

Occurrence. Green River, Colorado-Utah: U.C. Mus. Pal., hypotype 20671.

Pinus kelloggii Webber, Carnegie Inst. Wash. Publ. 412: 121, pl. 1, figs. 1–3, 1933. Ricardo, California. U.C. Mus. Pal., cotypes 156A–C.

Fossil wood from the lower part of the Ricardo Formation (12 Ma), Last Chance Gulch, on the south slope of the El Paso Mountains 40 km northeast of Mohave, California, has been identified as that of piñon. The associated flora includes woods of palm, oak, cypress, and locust.

Pinus kinnickensis Axelrod, sp. nov. TYPE: U.S.A. California: Tehachapi. U.C. Mus. Pal. holotype 1399. Figure 21*a*.

Pinus lindgrenii Knowlton. Axelrod, Carnegie Inst. Wash. Publ. 512: 85, 1939.

Seed ovoid in shape with an obtuse apex and rounded base, somewhat asymmetrically swollen, 1 cm long and 5 mm wide; testa very thin, and in one or two areas the papery nucellus still evident; endosperm with the contained embryo 7 mm long and 3 mm broad; oblong, rounded at one end and tapering at the other.

Discussion. During collecting of the Tehachapi flora, situated at the southeast end of the Sierra Nevada, a complete pine nut was uncovered in the andesite tuff that overlies the rhyolite tuff bed in which the fossil leaves occur. The specimen was identified as *P. lindgrenii* because at that time it was the only fossil piñon known and the pine nut seemed referable to it. Now that more numerous cones of *P. lindgrenii* are available (see below), it is evident that that species has much larger seeds than the Tehachapi specimen. It therefore represents a different species and is given a new name.

The complete specimen cannot now be illustrated because over the years the tuff in which it occurs has largely disintegrated, leaving only an impression of one side of the seed. Figure 21*a* shows the specimen in both concave and convex views.

Pinus lindgrenii Knowlton, Torreya 1: 113–115, text figs. 1–3, 1901. TYPE: U.S.A. Idaho: Chalk Hills. U.S. Nat. Mus. holotype 8179. Figures 17–21.

The silicified cone collected by one of Lindgren's associates, and described by Knowlton, comes from a site south of Bruneau, southern Idaho. It is from the Chalk Hills Formation (Malde & Powers, 1962) that has yielded diverse mammals that are judged to be Late Miocene (Hemphillian), or about 6–7 Ma. Other fossil plants in the formation include a bracket fungus and woods identified as fir, oak, alder, poplar, and hickory (Brown, 1940).

Additional cones collected by Ruth A. Kirkby add importantly to our understanding of the species and its position in the Subsect. *Cembroides.* Her collections come from the north end of Chalk Hills (sec. 19) and west of Highway 51 in sec. 25, T. 7 S, R. 4 E.

Supplementary description. Ovuliferous cones ovate to ovoid, base truncate, tip acute to obtuse; 5.0–7.0 cm long and 4.0–6.0 cm broad; cone scales thick, up to 2.5 cm broad in middle of cone, smaller elsewhere, the scales with low, broadly triangular apophyses; umbo centro-parvi-mucronate. Seeds wingless, very large, some in middle of cone 2.5 cm long, crudely tear-shaped, broader distally, larger than those of piñon today; shell of seed very thin.

Discussion. *Pinus lindgrenii* is generally allied to *P. cembroides* and *P. edulis* in that they also have low, triangular apophyses. However, their cones are smaller and the seeds are not so large as those of the fossils. *Pinus monophylla* and *P. quadrifolia* both differ from *P. lindgrenii* in that they have more prominent, raised apophyses, and also smaller cones and seeds. Cones of *P. pinceana* of the Sierra Madre Oriental are most similar to the fossil, though *P. lindgrenii* may represent a species intermediate between *P. pinceana* and a *P. cembroides-edulis* alliance.

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FIGURES 19–24.—19–21. *Pinus lindgrenii* Knowlton. Chalk Hills, Idaho. Jurupa Cultural Center, Riverside, California. Hypotypes 11200, 11201, 11204. Late Miocene, 5–6 Ma.—21*a*. *Pinus kinnickensis* Axelrod. Tehachapi, California. U.C. Mus. Pal., holotype 1399. Oriented to show concave and convex views.—22–24. *Pinus balfouroides* Axelrod. Thunder Mountain, Idaho. U.C. Mus. Pal., hypotypes 7186–7188. Middle Eocene, 45 m.y.

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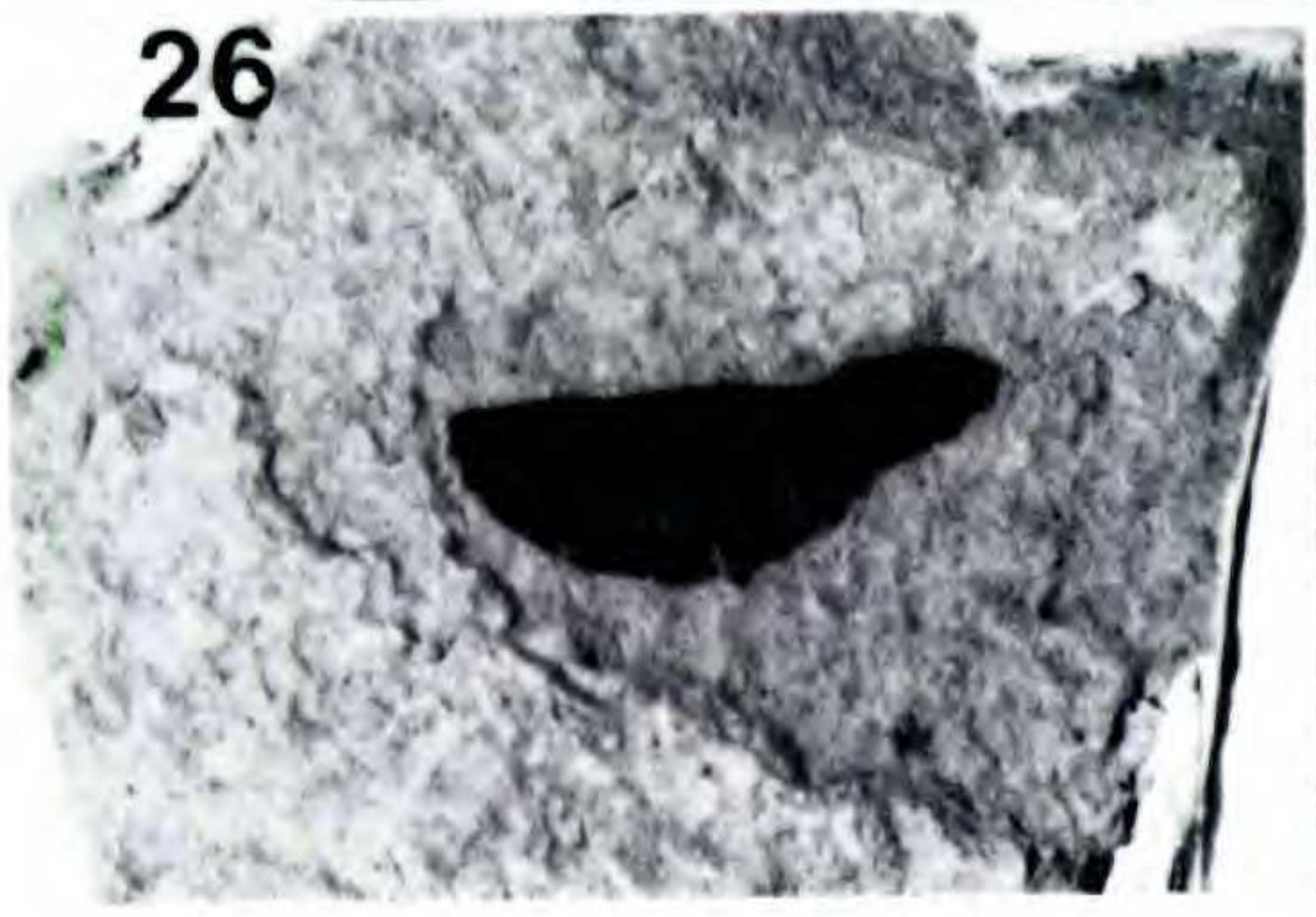

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The question may be raised as to whether the larger, more prominent, upswept apophyses of *P. monophylla* and *P. quadrifolia* reflect adaptation to a drier summer climate in the west. Some indication of this is seen in the western Arizona populations of *P. edulis* that have larger apophyses.

Occurrence. Chalk Hills, Idaho: Jurupa Mus. Nat. Hist., Riverside, California, hypotypes 11201, 11203–11205, homeotypes 11202–11206.

Pinus sanjuanensis Axelrod, sp. nov. TYPE: U.S.A. Colorado: Creede. U. Colo. Mus., holotype 19701; U.C. Mus. Pal., paratypes 7239–7244, 7247. Figures 12–16.

Imprint of near-proximal portion of globular cone; measures 4.0 by 4.5 cm in section; apophyses subdued; umbro mucronate, centro in position on scales; terminal ends of scales chiefly 5-sided and asymmetrically so; fascicles in 2s; 1.5–3.2 cm long, individual needles 1 mm wide, slightly curved; tips tapered to a sharply acute tip; base is a subdued, rounded remain of the deciduous sheath.

Discussion. The imprint of the cone cannot be separated from those of modern *P. edulis* cones. Needles in 2s occur at the Dry Creek localities, but were encountered only rarely at other sites. They are also comparable to those of the living *P. edulis* of the southern Rocky Mountains and northern Mexico. Many of its present associates have allied taxa in the Dry Creek florules, including species of *Cercocarpus, Fallugia, Holodiscus, Mahonia, Peraphyllum, Philadelphus, Quercus, Ribes, Robinia, Sapindus,* and others. The Dry Creek area has the best representation of vegetation of semiarid requirements in the Creede basin consistent with the occurrence of piñon there.

In her report on the Creede flora, Stewart (1940: 146) referred to fossil wood identified as a pine of the *Cembroides* alliance.

The only other pine in the Cordilleran region that seems related to this species is *P. ballii* Brown from the Green River flora, represented by a fascicle of three needles and a cone (MacGinitie, 1969). The 3-needled fascicle presumably is more nearly allied to *P. cembroides* which now ranges from southern Arizona into Mexico. The apophyses of the cone scales are more raised than those of *P. sanjuanensis.*

Subsect. *Balfourianae*

This small group includes *P. aristata* Engelm. of the central to southern Rocky Mountains, *P. longaeva* Bailey of the west-central Rocky Mountains and Great Basin ranges, and *P. balfouriana* Grev. & Balf., which is discontinuous from the Klamath Mountain area of northwestern California to the southern Sierra Nevada.

Pinus balfouroides Axelrod, Univ. Calif. Publ. Geol. Sci. 121: 209, 1980. TYPE: U.S.A. Nevada: Chalk Hills. U.C. Mus. Pal., holotype 8007, paratypes 8009–8013. Figures 22–33.

Pinus florissanti Lesquereux. Axelrod, Univ. Calif. Publ. Geol. Sci. 39: 227, pl. 42, fig. 9, 1962.
Pinus wheeleri Cockerell. Axelrod, ibid., p. 227, pl. 42, figs. 4–8, 1962.
Pinus quinifolia Smith. Axelrod, Ann. Missouri Bot. Gard. 63: 28, figs. 13–14, 1976.
Pinus sp. Brown, U.S. Geol. Surv. Prof. Paper 186-J: 167, pl. 45, fig. 9, 1937.

The above-listed material from the Purple Mountain (13 Ma) and Chalk Hills (12 Ma) floras, western Nevada (Axelrod, 1976, 1962), includes cones, winged seeds, and needles in 5s. They are similar to structures produced by *P. balfouriana* of high montane regions in California.

A new locality for the species is in the Middle Miocene Temblor Formation (15 Ma) at Sharktooth Hill, near Bakersfield, California (Fig. 29). In addition, numerous fascicles and a cone scale of the species are in the Coal Creek flora, Idaho (Fig. 30–33) dated at 29 Ma. Associated are species of *Abies, Larix, Picea, Pinus, Sequoiadendron, Chamaecyparis,* and diverse deciduous hardwoods, including *Acer, Betula, Carya, Cornus, Crataegus, Malus, Sassafras, Sorbus,* and *Zelkova.* Furthermore, impressions of cones and needles in 5s that represent *P. balfouroides* are in coarse, silicified sedimentary rocks at Dewey

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FIGURES 25–33.—25–27. *Pinus balfouroides* Axelrod. Purple Mountain, Nevada. U.C. Mus. Pal., hypotype 7177, 7178, 5501. Late Miocene, 13 Ma.—28. *Pinus balfouroides* Axelrod. Chalk Hills, Nevada. U.C. Mus. Pal., holotype 8007. Late Miocene, 12 Ma. (From Axelrod, 1962.)—29. *Pinus balfouroides* Axelrod. Sharktooth Hill, California. U.C. Mus. Pal., hypotype 7180. Middle Miocene, 15 Ma.—30–33. *Pinus balfouroides* Axelrod. Coal Creek, Idaho. U.C. Mus. Pal., hypotypes 7182–7185. Late Oligocene, 27 Ma.

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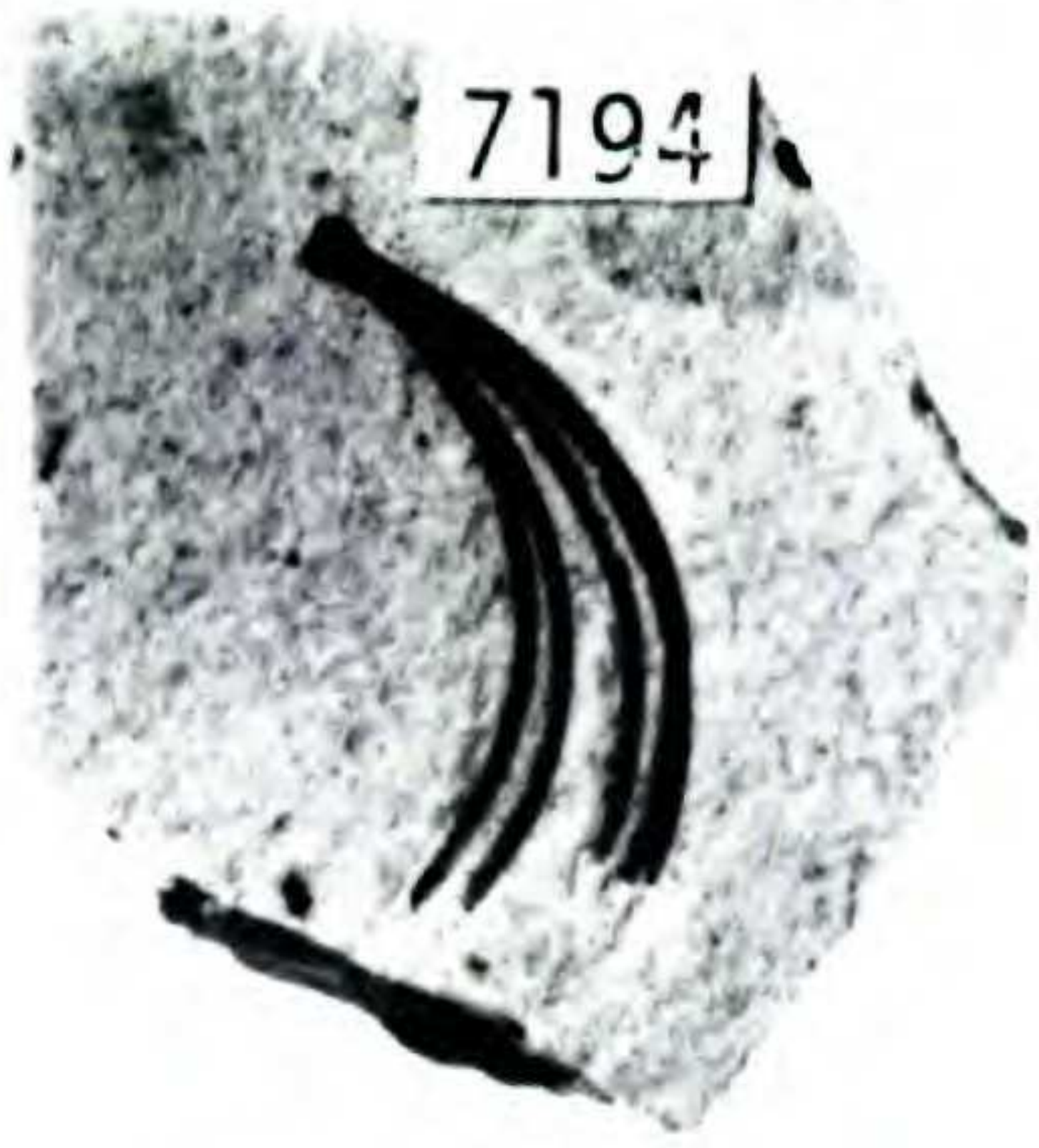

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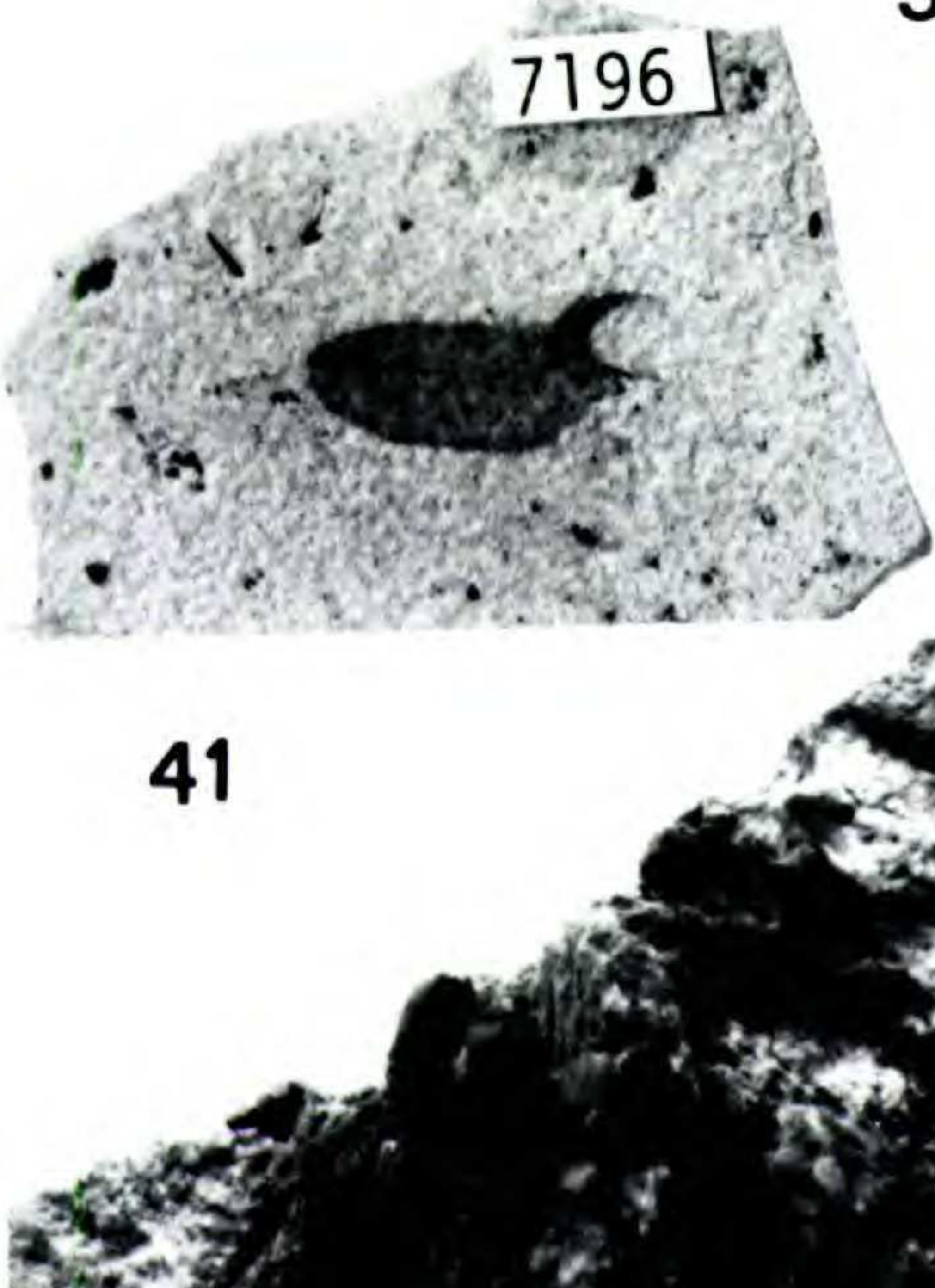

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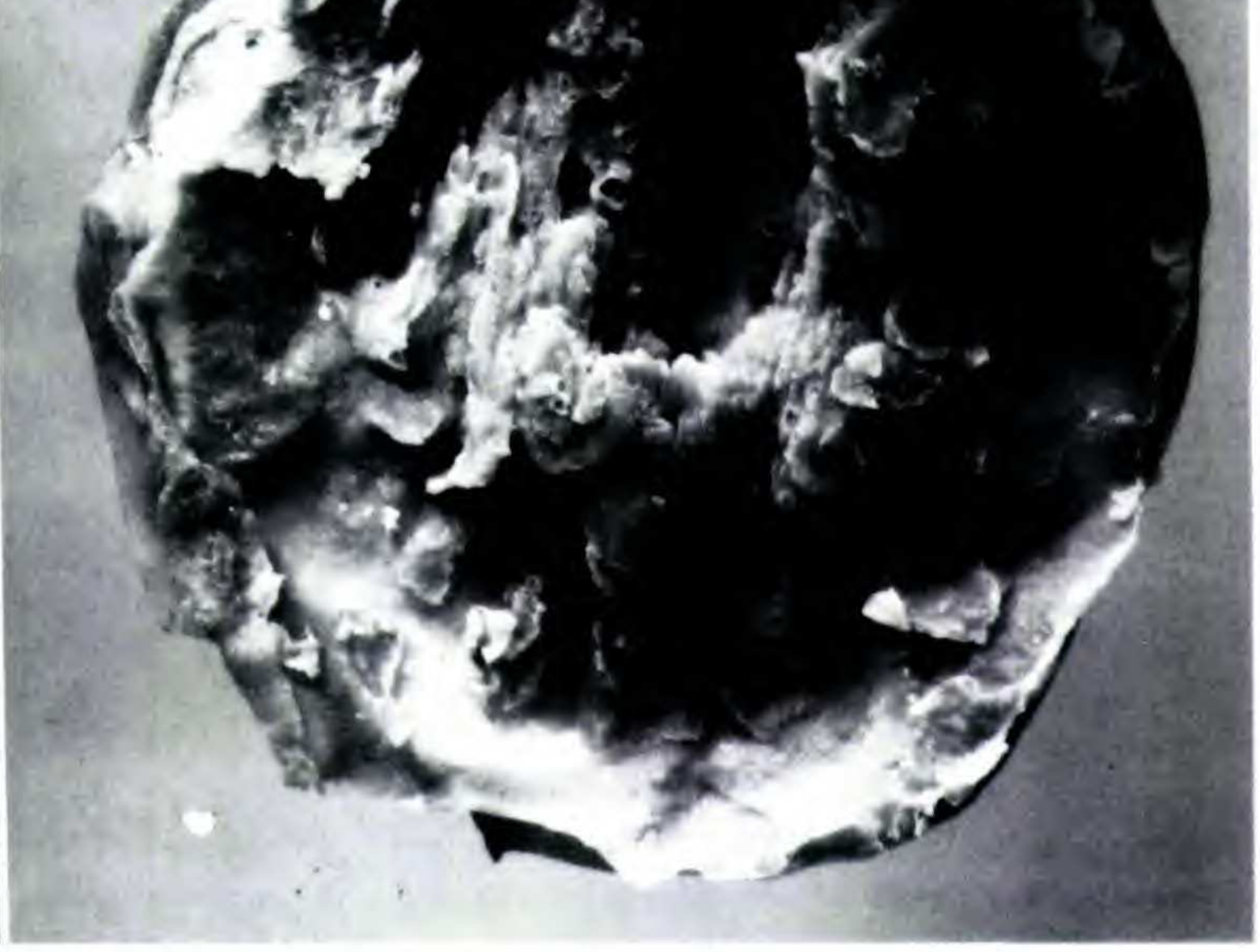

Mine, Thunder Mountain, central Idaho (Figs. 22–24). Now at an altitude of 2,300 m, the fossils are in the Dewey Beds, a volcaniclastic subunit eroded from Sunnyside Rhyolite of the Challis Volcanics, and dated at ca. 46 Ma (Leonard & Marvin, 1984). The associated flora (Brown, 1937) is largely coniferous. It includes cones and foliage of *Abies, Larix, Picea, Pinus,* and *Sequoia,* as well as a few rare shrubby species of *Comptonia, Salix* and *Vaccinium.* The assemblage suggests a high montane environment, probably near 1,300 m.

Additional specimens from the Purple Mountain flora are also illustrated (Figs. 25–27). These occur with mixed conifer forest taxa, notably species of *Abies, Picea, Pinus, Chamaecyparis, Pseudotsuga,* and *Sequoiadendron* that lived near broadleaved sclerophyll vegetation composed of species of *Arbutus, Cercocarpus, Chrysolepis, Heteromeles,* and *Quercus.*

Occurrence. Purple Mountain, Nevada: U.C. Mus. Pal., hypotypes 5501–5502, 7177–7179; Sharktooth Hill, California: U.C. Mus. Pal., hypotype 7180; Coal Creek, Idaho: hypotypes 7182–7185; Thunder Mountain, Idaho: U.C. Mus. Pal., hypotypes 7186–7188; U.S. Nat. Mus. hypotype (unnumbered).

Pinus crossii Knowlton, U.S. Geol. Surv. Prof. Paper 131-G: 185, pl. 41, figs. 3, 8–10, 1923. Creede, Colorado. U.S. Nat. Mus., holotype 36514, paratypes 36511–36513. Figures 34–42.

Pinus crossii Knowlton. Axelrod, Univ. Calif. Publ. Geol. Sci. 59: 62, pl. 7, figs. 6–9, 1966. Bailey, Ann. Missouri Bot. Gard. 57: figs. 34–37, 1970.
Pinus aristata crossii Cockerell, Nature 133: 573, fig. 1, 1933.

Supplementary description. Cones long ovate, 8 to 10 cm long and 4.5 cm broad (closed in water); cone scales with long, sharp, upcurved prickles; needles in 5s, 1.1–3.0 cm long, with a conspicuous single groove present in the distal part; the needles on branchlets are crowded and bunched to give a fox-tail appearance; seed wings open, 1.2–2.0 cm long, the wing generally long oval, distal end rounded, 6–7 cm broad.

Discussion. The short, curved fascicles with needles in 5s that Knowlton named *Pinus crossii* are supplemented now by large suites of fascicles, branchlets with clusters of needles, winged seeds, and impressions of pine cones. All of this material is allied to *P. aristata* Engelm. of the southern Rocky Mountains in Colorado and northern New Mexico. However, there are sufficient differences to indicate that *P. crossii* probably is ancestral to the living bristlecone pine. The fossil cones are generally more robust and broader (as measured when closed in water) and also average larger, with most reaching 7.5 to 9.5 cm long and up to 4.5 cm broad. Furthermore, the fragile prickles, where well preserved, evidently were longer, for some are up to 8 mm long. Another difference is in the seed wing, which is broader and the seed, which is larger, than in most populations of *P. aristata* today.

The differences may be attributed to a more genial climate at the close of the Oligocene, with a longer growing season, more moisture, and milder temperature. It is noted that the abundant remains of *P. crossii* are associated with woodland taxa, notably species of *Chamaebatiaria, Cercocarpus, Fallugia, Juniperus, Peraphyllum, Mahonia,* and other members of that community. By contrast, *P. aristata* is confined now largely to drier, rocky sites at subalpine levels, reaching down on drier sites into the middle of the mixed conifer belt, well removed from piñon-juniper woodland vegetation today.

Occurrence. Creede, Colorado: U.C. Mus. Pal., hypotypes 7190–7198, homeotype 7246; U. Colo., hypotypes 18654, 19694, 19698, homeotype 19701; Copper Basin, Nevada: U.C. Mus. Pal., hypotypes 8873–8876, 8901, 8902; Titus Canyon Formation, Death Valley, California: U.C. Mus. Pal., hypotype 7189.

SUBGENUS PINUS

SECT. TERNATAE

Subsect. *Leiophyllae*

Pinus coloradensis Knowlton, U.S. Geol. Surv. Prof. Paper 131-G: 186, pl. 41, fig. 6. 1923. TYPE: U.S.A. Colorado: Creede. U.S. Nat.

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FIGURES 34–42.—34–40. *Pinus crossii* Knowlton. Creede, Colorado. U.C. Mus. Pal., hypotypes 7190, 7191, 7193–7196, 7198. Late Oligocene, 26.5 Ma.—41, 42. *Pinus crossii* Knowlton. Titus Canyon, Death Valley, California. U.C. Mus. Pal., hypotype 7189. Figure 42 is a latex cast of Figure 41. Early Oligocene, ca. 37 Ma.

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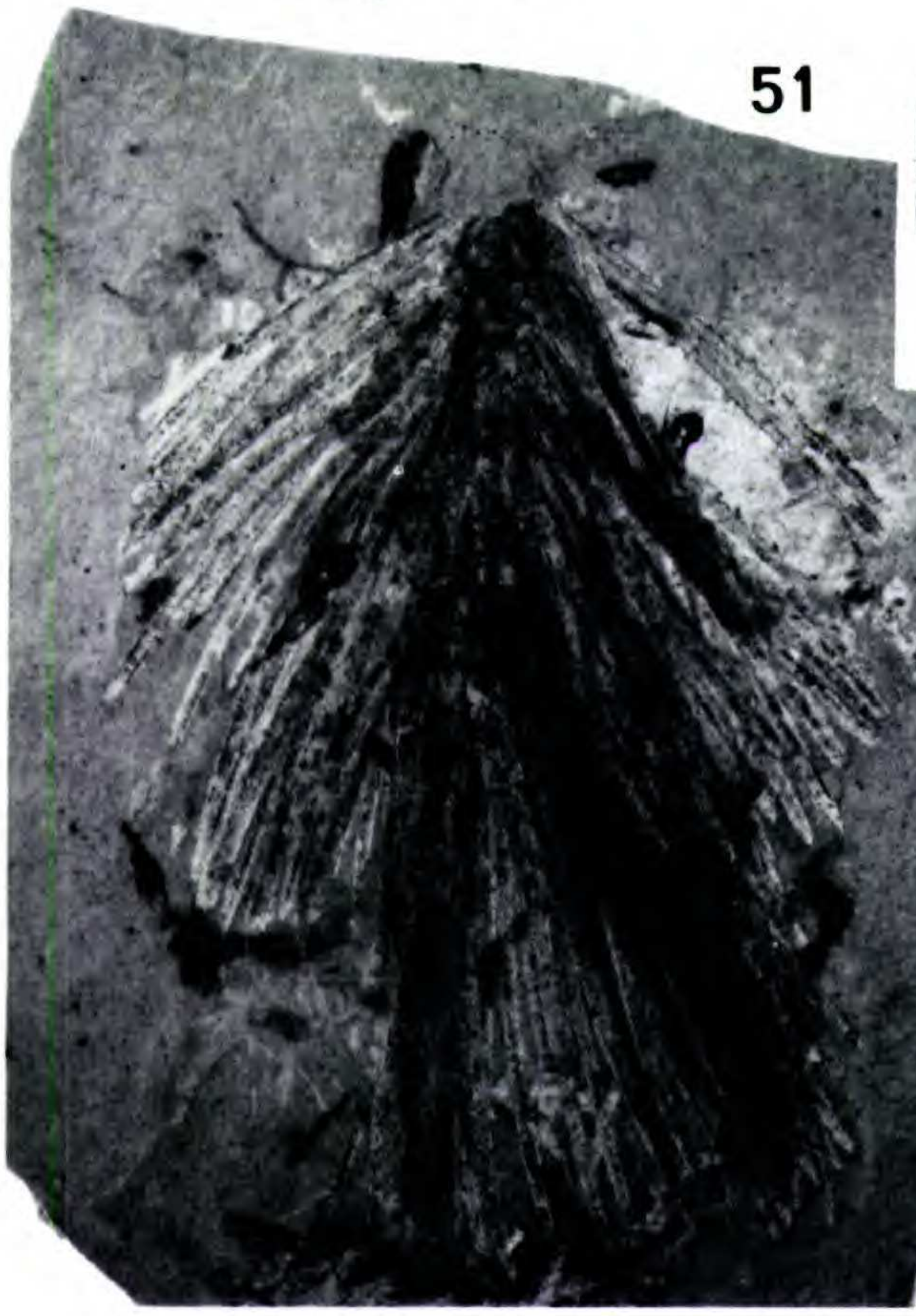

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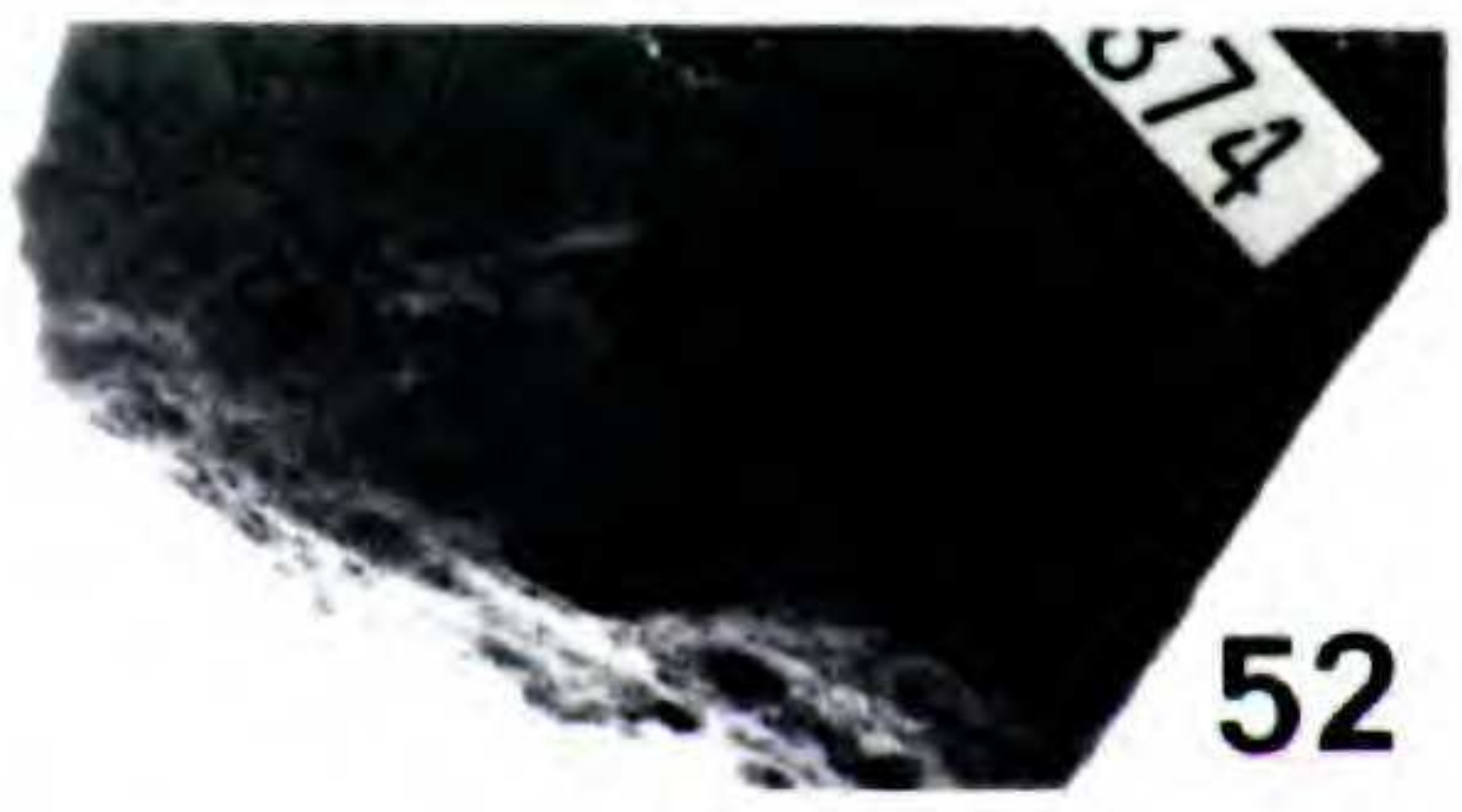

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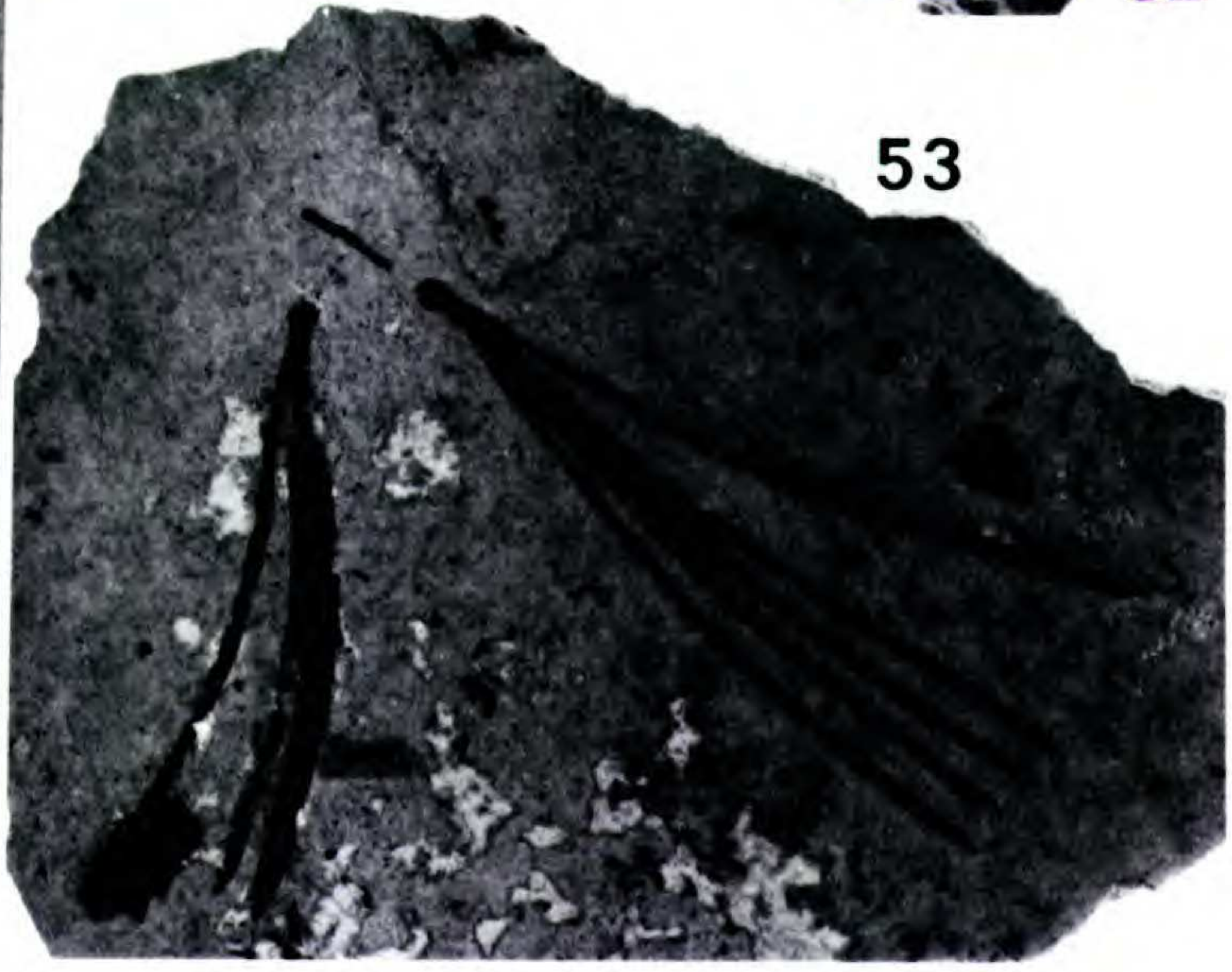

Mus., holotype 36506. Figures 43–45, 47–53.

The type specimen was incorrectly illustrated. The cone scales are thin, not swollen as the retouched figure suggests. The following supplementary description is based on the type and an additional cone in the Univ. Colorado Museum, as well as foliage and winged seeds presumed to represent this species.

Supplementary description. Cones small, oval to elliptic in outline, truncate proximally, broadly obtuse distally, 3.0–4.5 cm long, 2.0–3.0 cm broad (open); cone scales thin, tips broadly rounded, slightly widened distally, and somewhat reflexed when open; umbo dorsal, centro erecto-mucronate. Needles in 5s, quite slender, 4–5 cm long, 0.5–1.0 mm broad, tapered distally to acute tip, base with small, rounded (deciduous) sheath. Winged seeds 2.0–2.1 cm long, seed wing narrow, 5–6 mm broad, elliptic, distal and rounded to blunt; seed 3–4 mm long, ovate, acute tip, rounded proximally.

Discussion. Knowlton (1923) suggested a general similarity between *P. coloradensis* and cones of *P. arizonica* Engelm. However, *P. arizonica* cones are larger, the cone scales are broader, and the cone is overall more massive. Closer relationship appears to be with *P. chihuahuana* Engelm. (= *P. leiophylla* var. *chihuahuana*), which ranges from southern Arizona to central Mexico, though needles of the fossil are somewhat shorter. Its occurrence at Creede is consistent with a number of Madrean taxa in the flora, including species of *Arbutus, Cercocarpus, Fallugia, Mahonia,* and *Populus* that range from Arizona well south into Chihuahua and Durango. *Pinus chihuahuana* is a common member of the middle and upper woodland belt, as well as the mixed-conifer forest zone, relations consistent with the nature of vegetation in the Creede flora.

Occurrence. U. Colo. Mus., hypotype 27381; U.C. Mus. Pal., hypotypes 7199–7202.

Pinus paucisquamosa Templeton, South. Calif. Acad. Sci. Bull. 52: 64–66, figs. 1, 2, 3b, 1953. TYPE: U.S.A. California: Altamira Shale, Nat. Hist. Mus. Los Angeles Co., holotype 1400. Figure 46.

This small, nearly complete cone is from the upper Altamira Shale at Point Fermin, San Pedro, California. It occurs in the *Bolivina modeloensis* foraminiferal subzone, of early Mohnian age, or about 14.5 Ma. (Woodring et al., 1946; Turner, 1970). It was initially compared by Templeton (1953) with *Pinus chihuahuana,* but Mirov (1967: 35) suggested that it may be a species of Sect. *Insignes,* described and illustrated by Shaw (1914). *Insignes* are now considered a heterogeneous group, comprising species of *Sylvestres* (*P. halepensis, P. pinaster*), *Australes* (*P. rigida, P. serotina, P. pungens*), *Contortae* (*P. virginiana, P. clausa, P. banksiana, P. contorta*), and *Oocarpae* (eight species, four of each in California and Mexico). Comparison with cones of these species reveals little evidence of relationship with *P. paucisquamosa.*

As suggested by Templeton, the fossil resembles the smaller cones of *P. chihuahuana* (= *P. leiophylla* Scheide & Deppe var. *chihuahuana*), which ranges from southern Arizona-adjacent New Mexico southward into central Mexico. However, in its broader cone scales the fossil shows greater relationship with cones of *P. lumholtzii* Robinson & Fernald, distributed from Sonora southward into Jalisco. *Pinus paucisquamosa* probably is an extinct member of the Leiophyllae.

This pine occurs in the marine Altamira Shale, which includes glaucophane schist debris similar to that in the Poway Formation. Both sites derived this debris from the landmass Catalinia, which then stood near the present shore (Reed, 1951: 170–171; Woodford et al., 1954: 71, 74; Woodring et al., 1946). Since the basement terrane west of the Inglewood-Newport fault, where the fossil occurs, differs significantly from that to the east, considerable displacement is implied. This most probably was from Mexico, because Miocene rocks similar to those of the Poway occur south of Ensenada and also on South Coronado Island (Stuart, 1974). The relationships

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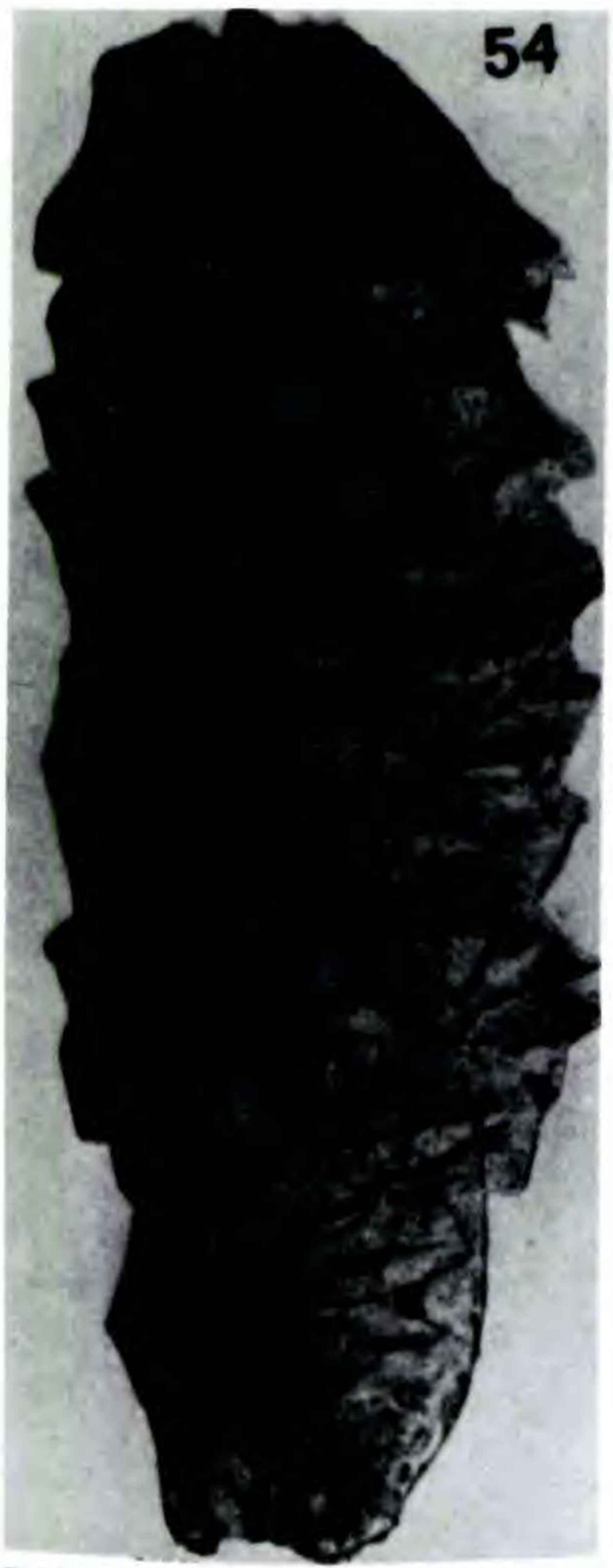
FIGURES 43–53.—43. *Pinus coloradensis* Knowlton. Creede, Colorado. U.S. Nat. Mus., holotype 365061. Latest Oligocene, 26.5 Ma. (Previously figured by Knowlton, 1923.)—44. *Pinus coloradensis* Knowlton. A latex cast of specimen in Figure 43.—45. *Pinus coloradensis* Knowlton. Creede, Colorado. Univ. Colo. Mus., hypotype 27381. Latest Oligocene, 26.5 Ma.—46. *Pinus paucisquamosa* Templeton. Altamira Shale, California. Nat. History Mus. Los Angeles Co., cast of holotype A4432/PB-1400. Middle Miocene, 15 Ma.—47–53. *Pinus coloradensis* Knowlton. Creede, Colorado. U.C. Mus. Pal., hypotypes 7273, 7202, 7376, 7278, 7200, 7374, 7201. Latest Oligocene, 26.5 Ma.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suggest that the Miocene fossil site was then opposite western Sonora where members of Subsect. *Leiophyllae* occur today, and probably did in the Middle Miocene (ca. 15 Ma).

SECT. PINUS

Subsect. *Sylvestres*

This alliance has 19 living species of which 11 are Asiatic, six European, and two American. The last include *P. resinosa* Aiton of the northeastern United States and adjacent Canada, and *P. tropicalis* Morelet of Cuba and Isle of Pines.

Several present European species reportedly have allied fossils in that region (see Mirov, 1967; Gaussen, 1960), but taxa of the alliance in North America are now known as fossil from only the Middle Eocene Allenby Formation (46 Ma) near Princeton, British Columbia (Stockey, 1984). Stockey analyzed the internal structure of cones and needles preserved in chert and showed that three taxa have the basic characters of *Sylvestres*. These include cones of *P. princetonensis* Stockey and *P. arnoldii* Miller and needles of *P. allisonii* Stockey. Whether these are to be grouped into a single species (*P. arnoldii* has priority) was left open by Stockey because the fossils are from different sites.

It is desirable to note that *P. clementsii* Chaney (1954) from the Late Cretaceous (85–86 Ma) of southern Minnesota was compared with *P. resinosa* Aiton. Examination of the mold that represents the type specimen (Chaney, 1954, figs. 1, 2) and a cast of it (Chaney, 1954, fig. 3) shows that the apophyses are raised and essentially convex. The structure of the umbo is largely erased, either by erosion or by weathering. Actually, there is insufficient detailed structure preserved to definitely relate the pine to a subsection. Furthermore, the paratype, which is from a locality some 25 miles distant, is only a small piece of a cone imprint. It certainly represents a different species as judged from the size and shape of the apophyses and the features of the umbo. It may represent a species of *Sylvestres* but is too incomplete for this to be certain. That either specimen is a pine can be disputed because their internal structure is indeterminate; both may be *Pityostrobus.*

From an ecological standpoint, the large dicotyledon leaves in the associated fossil flora indicate a warm temperate to subtropical climate (Chaney, 1954). If relationship with *Pinus resinosa* is accepted, it would be necessary to reconstruct high relief (1,000–1,500 m) in the region to provide a cold temperate climate for the pine. This would involve miles of transport via river, and, in view of the coarse grit and conglomerate in the section, the cones should be well worn, yet this is not the case. The evidence suggests that the *Pinus* (or *Pityostrobus*) species from southern Minnesota probably were members of the lowland flora, living on well-drained, drier south slopes not far from the areas of plant accumulation.

Occurrence. Minnesota, Cretaceous: Univ. Minnesota, Dept. Botany Paleobot. Coll., holotype no. C 770 (from Ochs Clay pit near Springfield), paratype no. C 711 (from near New Ulm, 25 miles east).

Subsect. *Australes*

This group of 11 species occurs in the southeastern United States, the Bahamas, Cuba, Hispanola, and Central America (Critchfield & Little, 1966, map 18). Fossil cones reportedly allied to *P. taeda* and *P. rigida* recorded from the Miocene of western Europe (in Gaussen, 1960) need to be reexamined before they can be accepted as valid records of Australes in Europe. One fossil species is now known for the group in the southeastern states.

Pinus collinsii Berry, Torreya 36: 124–127, text-fig. 2, 1936. TYPE: U.S.A. Maryland: Calvert Formation. U.S. Nat. Mus., holotype unnumbered and missing. Figures 57–59.

Pinus collinsii Berry. Berry, Wash. Acad. Sci. Jour. 31: 506–508, figs. 1, 2, 1941. St. Marys Formation, Maryland.

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FIGURES 54–59.—54. *Pityostrobus lynnii* (Berry) Miller. Aquia Formation, Belvedere Beach, Virginia. U.S. Nat. Mus., holotype 222786. Paleocene, ca. 60 Ma. (From Berry, 1934.)—55. *Pinus engelmannoides,* sp. nov. Axelrod. Creede, Colorado. U.C. Mus. Pal., holotype 7203. Late Oligocene, 26.5 Ma.—56. *Pinus macginitieii,* sp. nov. Axelrod. Creede, Colorado. Univ. Colo. Mus., holotype 19703. Late Oligocene, 26.5 Ma.—57. *Pinus collinsii* Berry. Calvert Formation, Stratford Cliffs, Virginia. U.S. Nat. Mus., hypotype. Middle Miocene, 15 Ma. (From Berry, 1941.)—58. *Pinus collinsii* Berry. Calvert Formation, near Plum Point, Maryland. U.S. Nat. Mus., hypotype. Middle Miocene, 15 Ma. (From Berry, 1941.)—59. *Pinus collinsii* Berry. Calvert Formation, near Plum Point, Maryland. U.S. Nat. Mus., holotype. Middle Miocene, 15 Ma. (From Berry, 1936.)

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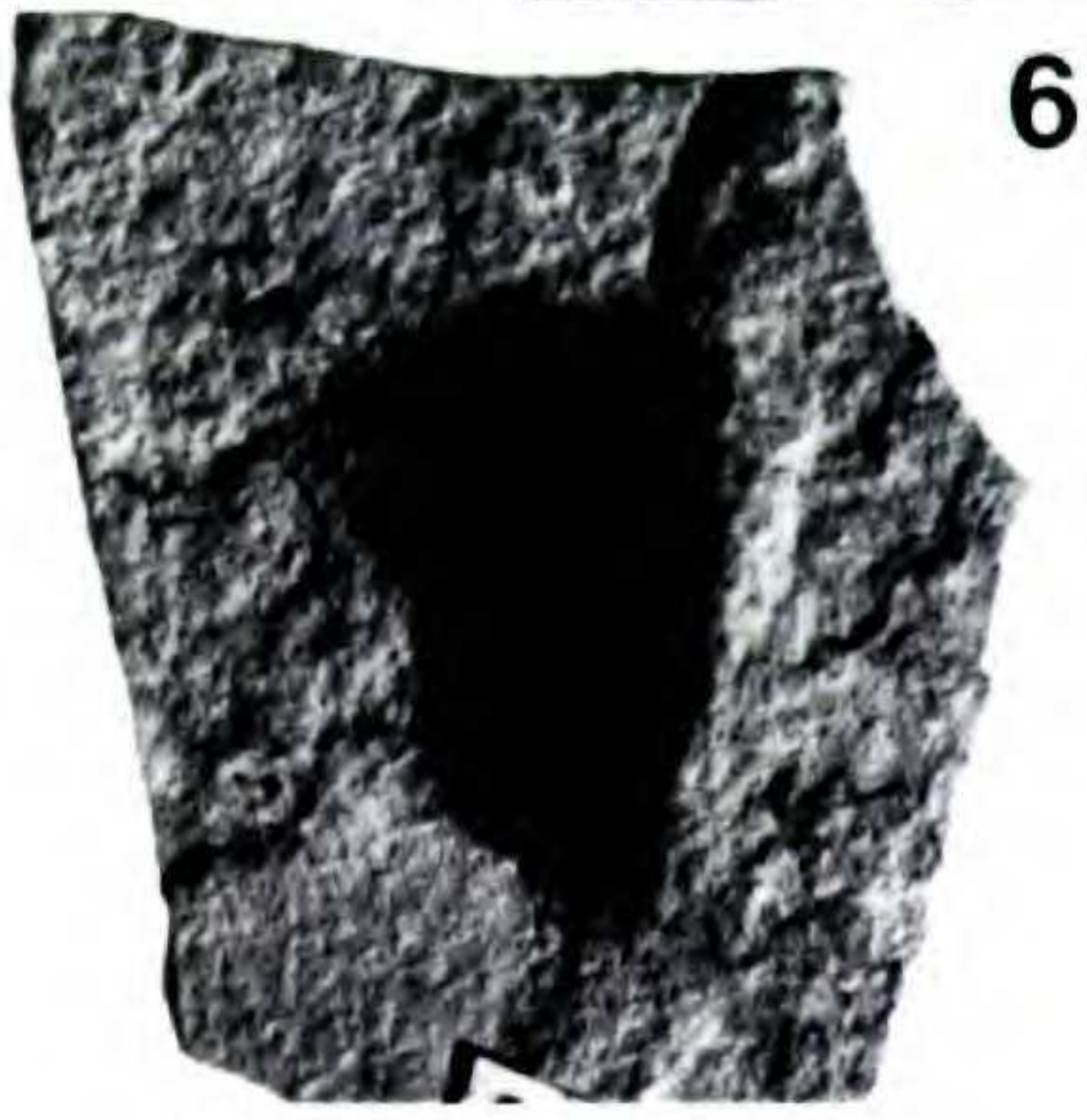

Cones recovered from the Middle Miocene Calvert and St. Marys Formations, Maryland, are similar to those of the living *Pinus taeda*, a widely-distributed species along the Atlantic and Gulf coastal plain from Delaware into eastern Texas. Associates of *P. collinsi* in the Calvert flora (Berry, 1916) include *Berchemia, Cassia, Nyssa, Platanus, Quercus, Salix,* and *Ulmus* that occur with *P. taeda* today.

Occurrence. St. Marys Formation, Maryland. U.S. Nat. Mus., specimen missing from collection and unnumbered.

Pityostrobus lynnii (Berry) Miller, Torrey Bot. Club Bull. 104: 5–9, figs. 1–7, 1977. *Pinus lynnii* Berry, Wash. Acad. Sci. Jour. 24: 182–183, fig. 1, 1934. TYPE: U.S.A. Virginia: Aquia Formation. U.S. Nat. Mus., holotype 22786.

The well-preserved cone described by Berry (1934), from the Aquia Formation, is now considered Paleocene in age (in Miller, 1977b). It has the external features of a species of *Australes* and resembles cones of *P. taeda* as well as those of *P. elliottii* Engelm. and *P. caribaea* Morelet, although the last two are on average larger than the fossil.

The internal structure of an additional cone studied by Miller (1977b) shows that it represents the extinct genus *Pityostrobus*. The bract-trace is free, and the scale has a thin, not a thick, vascular strand. Apart from these differences, in its general structure and shape it certainly seems to foreshadow pines of Subsect. *Australes* and may well have given rise to a species that produced cones similar to those of *P. taeda*.

Occurrence. Aquia Formation, Virginia: U.S. Nat. Mus., hypotype 201950.

Subsect. *Ponderosae*

This large group of living pines includes 13 species, most of which are in Mexico. A few fossil cones are known that resemble those of different species of the alliance. Identification of fossil winged seeds and fascicles poses a major problem, because those of many modern species are so similar that their reference to any one fossil species seems doubtful. In spite of the uncertainty, there are numerous records of large seed wings (without seeds) that appear to represent those similar to the western *P. ponderosa* Lawson. These have been recorded at several localities in the Rocky Mountains, including the Green River (46 Ma), Florissant (34 Ma), Ruby and Beaverhead (ca. 30 Ma), and Creede (26.5 Ma) floras. In the Great Basin, there are similar records in the Fallon (12 Ma), Middlegate (18 Ma) and Fingerrock (16 Ma) floras.

The following are records of fossil cones that appear to represent members of this subsection.

Pinus engelmannoides Axelrod, sp. nov. TYPE: U.S.A. Colorado: Creede. U.C. Mus. Pal., holotype 7203a, b. Figure 55.

Cone closed (in water), narrowly elliptic; 11–12 cm long, 4.5 cm broad proximally; broadly rounded or blunt proximally, apex acute; scales with prominent apophyses, asymmetrically triangular and upcurved; umbo apparently centro-reflexo-mucronate.

Discussion. This cone from the Creede flora resembles those produced by *P. engelmannii* Carr. in the Santa Rita and Chiricahua mountains, southeastern Arizona. It descends from the mixed-conifer forest zone to mingle with the middle to upper part of the oak woodland belt, an association similar to the vegetation setting at Creede. Among its associates at altitudes near 1,830 m (6,000 ft.) are *Pinus leiophylla, P. ponderosa, Pseudotsuga glauca, Juniperus deppeana, Arbutus arizona, Cercocarpus breviflorus,* and numerous oaks. From southern Arizona, *Pinus engelmannii* ranges southward in the Sierra Madre Occidental to Zacatecas, central Mexico.

Pinus macginitieii Axelrod, sp. nov. MacGinitie, Carnegie Inst. Wash. Publ. 599: 84, pl. 20, figs. 1, 3, 4, 1959. TYPE: U.S.A. Colorado: Florissant. U.C. Mus. Pal., lectotype 3776, paratype 3778; U.S. Nat. Mus., paratype 33758. Figures 56, 60–62.

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FIGURES 60–67.—60. *Pinus macginitieii* Axelrod, sp. nov. Florissant, Colorado. U.C. Mus. Pal., lectotype 3776.—61, 62. *Pinus macginitieii* Axelrod, sp. nov. Florissant, Colorado. U.C. Mus. Pal., paratype 3778, U.S. Nat. Mus., paratype 33758.—63–67. *Pinus ponderosoides* Axelrod, sp. nov. Creede, Colorado. U.C. Mus. Pal., holotype 7204, paratypes 7204–7208; Fallon Nevada, U.C. Mus. Pal., hypotypes 2034, 2035; Nevada, Aldrich Sta., U.C. Mus. Pal., hypotypes 4000, 4001.


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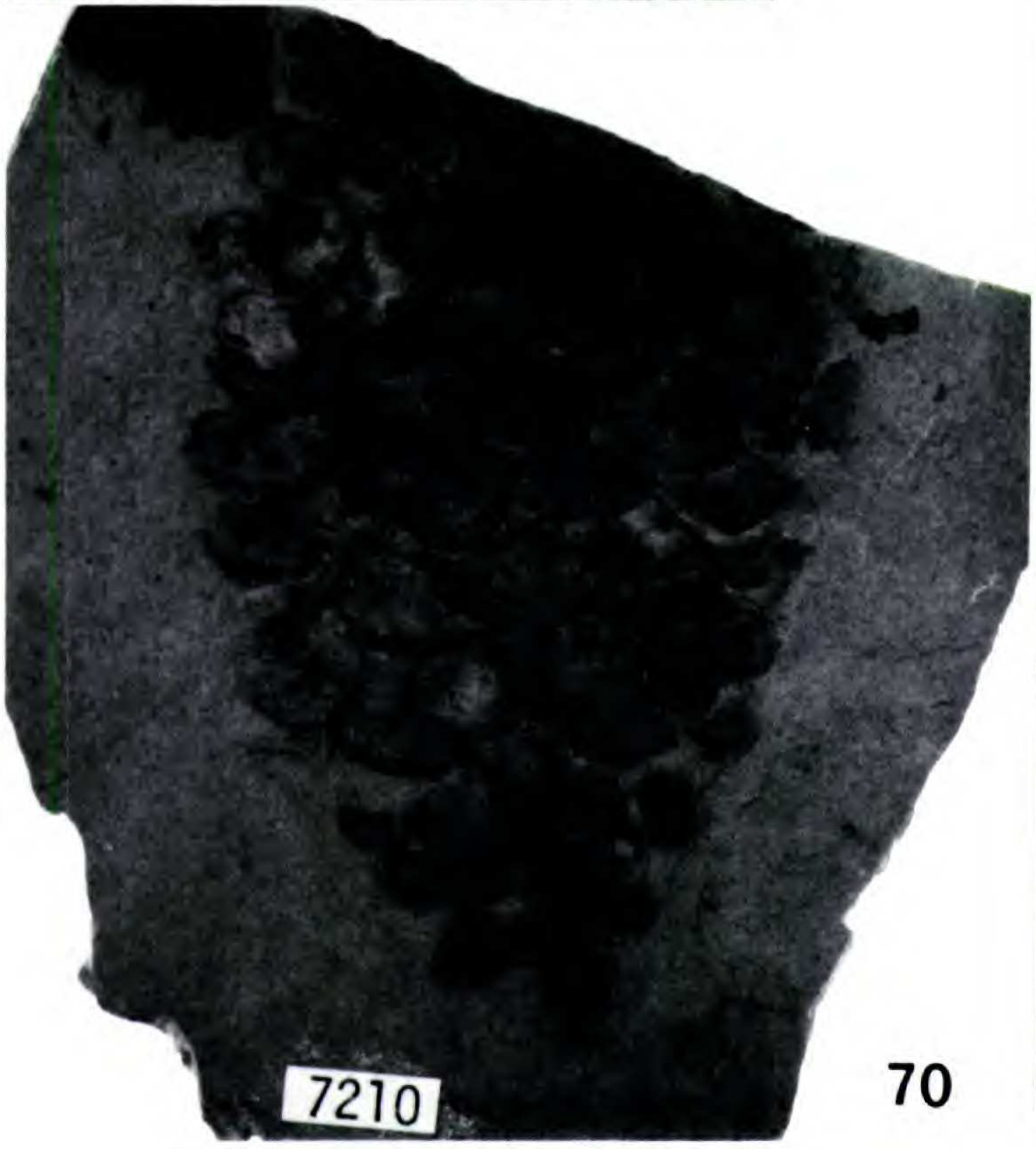

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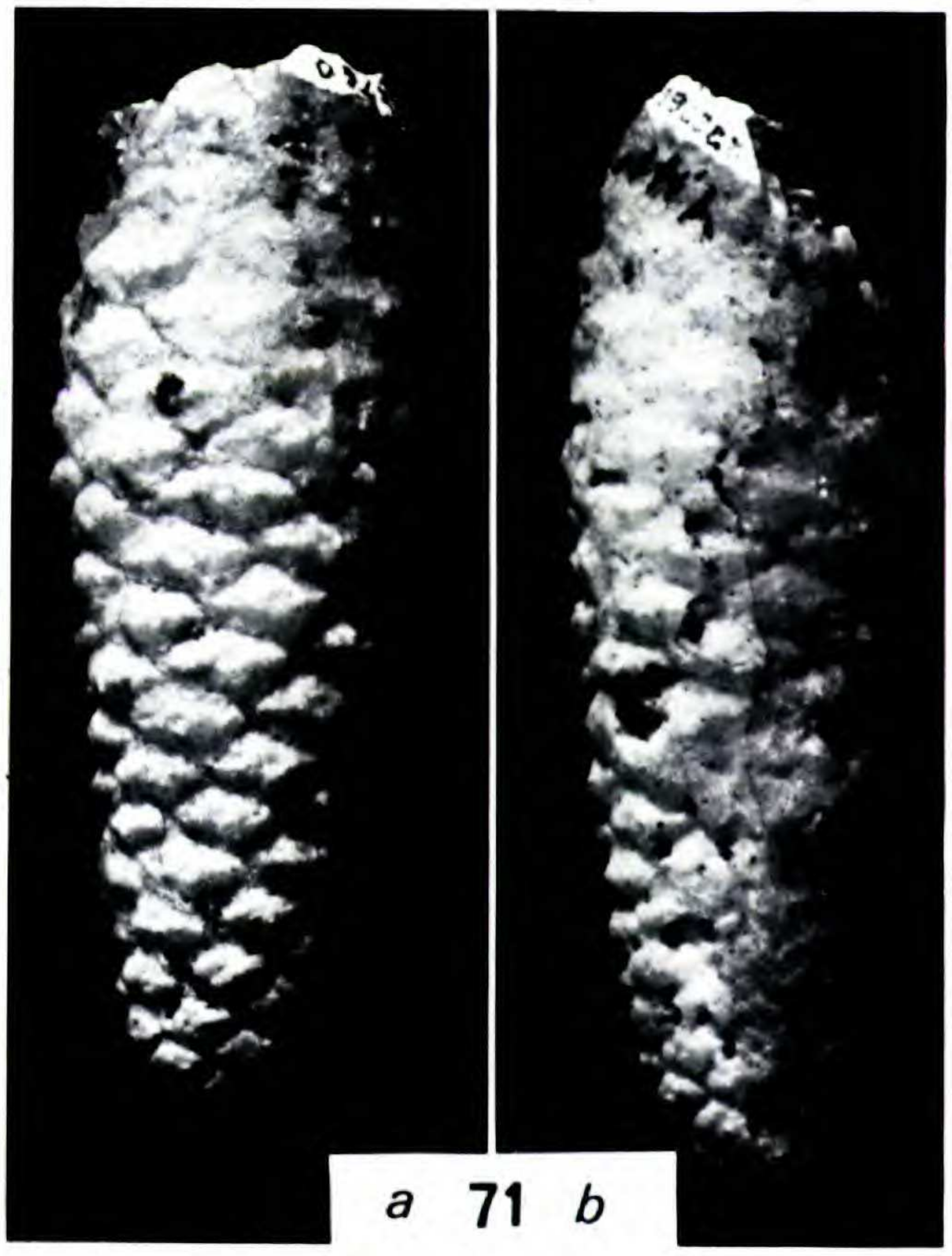
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Pinus florissanti Lesquereux. Becker, Palaeontographica 127-B: 61, pl. 6, figs. 3, 5, 6, 9 (not figs. 1–2, 4, 7–8, 10, which may be a different species), 1969.

The Florissant pine represented by long needles in 3s with a long persistent sheath, together with large seed wings is clearly of the *Ponderosae* alliance. Similar seeds in the Beaverhead flora (Becker, 1969) evidently represent the same species as does a single large seed wing in the Creede flora.

Needles in 3s, 17.5 cm or more long, with a large persistent sheath, needles grooved, 1–2 mm broad, tips acute; seed wings 2.5–3.7 cm long, 0.8–1.0 cm broad, tips rounded to asymmetrically acute; large seeds, ovate, 8–9 mm long and 4–7 mm broad.

Discussion. The above listed fossils do not represent *P. florissanti* because the type specimen is a cone similar to those of *P. flexilis.* It has needles in 5s, and the seed wings are attached to the scales. *Pinus macginitieii* is allied to species of Subsect. *Ponderosae,* but not to *P. ponderosa,* which has smaller winged seeds. Closer comparison may be made with *P. michoacana* Martinez, a species now in Mexico from Jalisco southward into Chiapas. The relation of the seeds to the large cones of *P. riogrande* in the Creede flora, which is compared with the living *P. montezumae* Lamb., is uncertain; they may be allied.

This species is named for Dr. Harry D. MacGinitie whose monographs on western Tertiary floras stand as excellent contributions to Tertiary paleobotany.

Occurrence. Beaverhead, Montana: N.Y. Bot. Gard., hypotypes 146a–b, 147, 144, 916; Creede, Colorado: Univ. Colorado Mus., hypotype 19703.

Pinus ponderosoides Axelrod, sp. nov. TYPE: U.S.A. Colorado: Creede. U.C. Mus. Pal., holotype 7204, paratypes 7206–7208. Figures 63–67.

Pinus florissantii Axelrod, Univ. Calif. Publ. Geol. Sci. 33: 276, pl. 4, figs. 19–20; pl. 17, figs. 10–11, 1956.

Cone fragment 7 cm long, scales 1.3–1.4 cm broad, 7–8 mm high, umbo centro mucronate, prickle upturned, sharp. Needles 8 cm or more long, fascicles in 3s with large persistent sheath, needles grooved, 1–2 mm broad, tips acute; seed wings 2.0–1.5 cm long, wing 6 mm broad, long elliptic, tip broadly rounded to bluntly acute; seed ovate, 4–5 mm long, 3–4 mm broad, dehiscent.

Discussion. The specimens of *P. macginitieii* in the Florissant flora cited above demonstrate that Subsect. *Ponderosae* was already in existence in the Eo-Oligocene transition. An older record of Subsect. *Ponderosae* is that of *P. premurrayana* Knowlton from the Absaroka Volcanics, of Middle Eocene age as noted below. Specimens in the Creede flora referred to *P. ponderosoides* seem more similar to structures produced by the *P. scopulorum* of the Rocky Mountains.

The relation of this species to other fossils—chiefly winged seeds—that have been compared with *P. ponderosa* is uncertain because most of them are difficult (or impossible) to separate from other members of the *Ponderosae.*

Occurrence. Fallon, Nevada: U.C. Mus. Pal., hypotypes 2034, 2035; Aldrich Station, Nevada: U.C. Mus. Pal., hypotypes 4000, 4001.

Pinus premurrayana Knowlton, U.S. Geol. Surv. Monogr. 32, pt. 2: 677, pl. 82, fig. 5, 1899. TYPE: U.S.A. Wyoming: Langford Formation. U.S. Nat. Mus., holotype 222760. Figure 71*a–b.*

This silicified cast of a cone recovered from the east side of Yellowstone Lake was compared by Knowlton with *P. murrayana.* It shows no relationship to cones of that species, either in size, shape, or the nature of the cone scales. The cone, refigured here in two views, appears to be a member of Subsect. *Ponderosae.* It resembles the slender cones of *P. lindleyii* Loudon (see Shaw, 1914, pl. 25, fig. 223), considered by some to be a variety of *P. montezumae* Lamb. It is also assigned to *Ponderosae* because woods representing two species of fossil pine from the Yellowstone fossil forest have characters that place them in the hard-pine group (Read, 1930), of which the *Ponderosae* are a part. In addition, needles of *P. iddingsii* Knowlton from the Yellowstone

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FIGURES 68–71.—68. *Pinus riogrande* Axelrod, sp. nov. Creede, Colorado. U. Colo. Mus., holotype 19704. Late Oligocene, 26.5 Ma.—69, 70. *Pinus riogrande* Axelrod, sp. nov. Creede, Colorado. U. Colo. Mus., paratypes 7209, 7210. Late Oligocene, 26.5 Ma.—71*a, b. Pinus premurrayana* Knowlton. Langford Formation, East of Yellowstone Lake, Wyoming. U.S. Nat. Mus., holotype 222,760. Two views of specimen. Early Middle Eocene, 50 Ma.

flora (Knowlton, 1899: 680, pl. 82, figs. 8, 9) are in 3s, are 13+ cm long, are rounded and flat on one side and channeled on the other. They are much like needles of *Ponderosae* today.

The precise site at which *P. premurrayana* was collected is unknown. However, discussion with J. Richmond of the U.S. Geological Survey and R. Baker, University of Iowa, both of whom have been actively engaged in the geology of the area, indicates that the fossil cone is from the Absaroka Volcanics. These contain much silicified wood on the east side of the Yellowstone Lake, whereas the Pleistocene (Sangamon) sedimentary rocks there have plant remains but they are not silicified. The volcanic rocks on the east side of the Yellowstone Lake represent the Langford Formation of the Absaroka Volcanic Supergroup, and are K/Ar dated at 50 Ma, or early Middle Eocene (*in* Smedes & Protska, 1972).

Pinus riogrande Axelrod, sp. nov. TYPE: U.S.A. Colorado: Creede. Univ. Colo. Mus., holotype 19704; U.C. Mus. Pal., paratypes 7209–7211. Figures 68–70.

Cones large, long elliptic to elliptic-ovate; complete specimen 12.3 cm long, 4.5 cm broad in middle; largest broken cone over 15 cm long and 6 cm broad; bluntly rounded apex and base; 9 × 11 rows of cone scales, the middle ones 1.5 cm broad, 1 cm high; umbo dorsal, centro-reflexed, short mucronate, prickles 2–3 mm long, directed distally.

Discussion. These large cones resemble those of the living *P. montezumae* Lambert, distributed now from Durango and Nuevo Leon southward into Guatemala. The modern species varies in cone and needle size with increasing altitude. As documented by Shaw (1914) and Martinez (1948), these structures decrease in size with altitude and have been described as a series of varieties. The fossils resemble cones from localities at moderate elevations, consistent with the ecology indicated by the Creede flora in which they occur.

Pinus truckeensis Axelrod, sp. nov. U.S.A. Nevada: Celetom Quarry. U.C. Mus. Pal., holotype 7223, paratype 7224. Figures 72*p*, *a* & 73.

Cone broadly elliptic in outline; base truncate, apex obtuse; 15 by 11 cm, with proximal end deciduous on branch, so cone probably up to 17 or 18 cm long; 12 × 14 rows of cone scales; those in middle of cone on symmetrical (posterior) side are 1.7–2.5 cm broad, on asymmetrical (anterior) side (1 cone only) 2 cm broad; apophyses broadly rhombohedral, symmetrical on one side (Fig. 72*p*), asymmetrical on the other and upswept (Fig. 72*a*); centro-mucronate and erect or reflexed; prickle not preserved.

Discussion. Two specimens are in the collection. The strongly asymmetrical cone was preserved as a mold diatomite. By gradually filling the cavity with latex, a cast of the entire cone was removed to display both sides (Fig. 72*p*, *a*). The other cone (Fig. 73) shows the complete face on the symmetrical (posterior) side. On its lower margin, evidence of asymmetry of the anterior side is evident. Both specimens are referred to one species.

The fossils resemble cones produced by *P. pseudostrobus* Lindl. The chief difference is that the fossil cones are somewhat larger than those in the collection available for comparison at the Institute of Forest Genetics, Placerville. In addition, the apophyses are proportionately larger. Otherwise, there appear to be no significant differences between these species. *Pinus pseudostrobus* ranges from the mountains of central Mexico to Chiapas and Guatemala, inhabiting the conifer forest and the oak-madrone woodland at altitudes from 2,300 to 3,200 m.

The occurrence of a pine of southern affinity in western Nevada is not unique for the area. Other taxa in the Miocene record there that have their nearest allies in the Southwest, or in adjacent Mexico, include species of *Arbutus, Bumelia, Cercocarpus, Fraxinus, Mahonia, Populus, Quercus,* and *Sapindus,* and they are more numerous in the Miocene of southeastern California.

The fossil cones occur in diatomite of the Coal Valley Formation, exposed at the Celetom Quarry of the Eagle-Picher Industries, 30 km east of Reno. The deposit is about 12.5 Ma old as judged from radiometric dates of closely associated rocks nearby.

Subsect. *Sabinianae*

There is only a very limited record of this group of large-coned pines represented now by three living species. *Pinus sabiniana* Doug. inhabits the foothills of the inner Coast Ranges of central and northern California and the lower west slopes

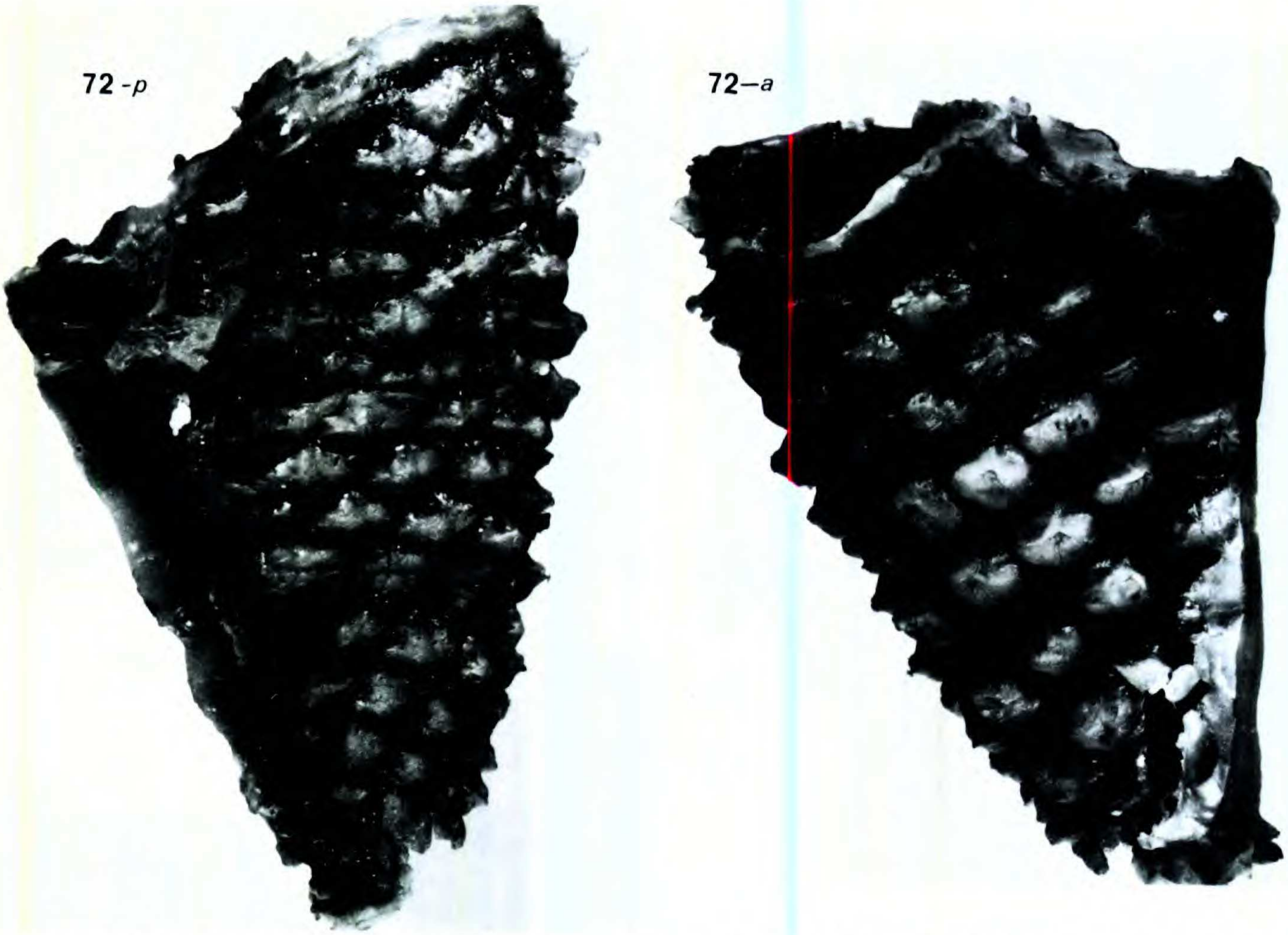


FIGURE 72. *Pinus truckeensis* Axelrod, sp. nov. Celetom Quarry, 30 km E. of Reno, Nevada. U.C. Mus. Pal., holotype 7223. Two views of specimen: *p, left* or posterior side; *a, right* or anterior side. Late Miocene, 12 Ma.

of the Sierra Nevada. *Pinus coulteri* D. Don occurs chiefly in the mountains of southern California at medium altitudes, ranging discontinuously northward in the Coast Ranges to Mount Diablo east of San Francisco Bay. *Pinus torreyana* Parry is a narrow endemic on the coast near La Jolla, and a subspecies occurs on Santa Rosa Island west of Santa Barbara (Haller, 1986).

The origin of the group is obscure but may lie with *P. oaxacana* Mirov of Mexico (Haller, 1966). It has similar cones as well as long needles in 5s. From this standpoint, there was an increase in cone size (*P. sabiniana, P. coulteri*) and the development of more armed cones with hooked apophyses. *Pinus oaxacana* occurs now in the Sierra Madre Occidental from Durango southward into Nayrit. In the early Neogene, forerunners of *P. torreyana,* as well as *P. sabiniana* and *P. coulteri,* may have separated from an ancestral *oaxacana*-like group and were then transported northward as the San Andreas fault system was activated (Crowell, 1979).

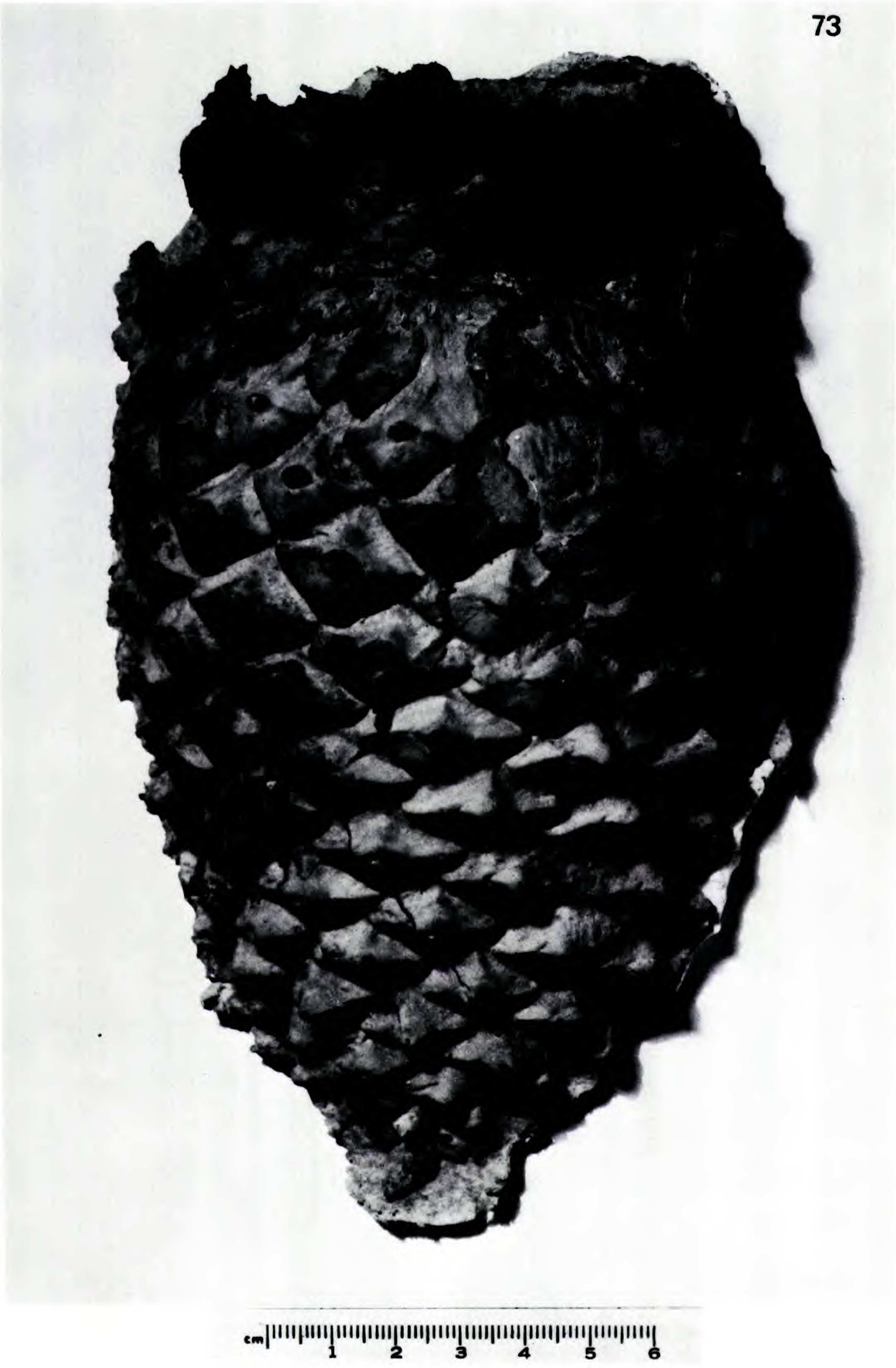
Mason (1927) identified specimens from the Bridge Creek and Cove Creek floras, Oregon, as *P. torreyana* Parry. However, these 5-needled fascicles with long, persistent sheaths are also similar to those of several *Ponderosae* taxa now in Mexico, as well as others (see Martinez, 1948).

Pinus hazenii Axelrod, Carnegie Inst. Wash. Publ. 476: 165, pl. 2, fig. 4, 1937. TYPE: U.S.A. California: Mount Eden. U.C. Mus. Pal., holotype 958, paratypes 7225, 7226. Figures 75, 76.

Very large cone scales, with large, hooked apophyses sharply constricted above suggest that this pine may be allied to *P. coulteri.* Additional material is needed to ascertain more definitively its relationship to that species.

P. coulteri produces one of the largest, most massive cones of living (and probably fossil) pines.

Pinus pieperi Dorf, Carnegie Inst. Wash. Publ. 412: 69, pl. 5, figs. 7–10, 1930. TYPE: U.S.A.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California: Pico Formation. U.C. Mus. Pal., holotype 305, paratype 304. Figure 74.

Pinus pieperi Dorf. Axelrod, Carnegie Inst. Wash. Publ. 476: 165, pl. 2, figs. 2, 3, 1937. Axelrod, Carnegie Inst. Wash. Publ. 590: 144, pl. 2, fig. 1, 1950. Axelrod & DeMéré, San Diego Mus. Nat. Hist. Trans. 20: 292, fig. E, 1984.

The above records of fossil digger pine are from the Pliocene and Late Miocene of southern California. *Pinus sabiniana* does not occur in that area today except at its northern margin in Santa Ynez Valley north of Santa Barbara and at the north end of Liebre Mountain, southeast of Tejon Pass. The species is recorded also in the Pleistocene of southern California at Seacliff (Axelrod, 1983), Carpinteria (Chaney & Mason, 1933), and Lake Canyon east of Ventura (Wiggins, 1951).

This species may have disappeared from southern California during the post-glacial Xerothermic period, which brought interior and semidesert species to the coastal strip (Axelrod, 1966: 42–55).

Occurrence. Anaverde Formation, California: U.C. Mus. Pal., hypotype 3269; Mt. Eden Formation, California: U.C. Mus. Pal, hypotypes 959, 960, 7227; Diego Formation, California: San Diego Mus. Nat. Hist., hypotype 25168.

Subsect. *Contortae*

This alliance includes four living species. Two are in the eastern United States, *P. clausa* (Chap.) Vasey of Florida and southern Alabama, and *Pinus virginiana* Miller of the Appalachian province. *Pinus banksiana* Lamb. ranges from the Lake States northward across Canada to the MacKenzie River and east to Nova Scotia. *Pinus contorta* Dougl. (with three vars.) occupies the Rocky Mountains north of southern Colorado (var. *latifolia*), extends down the Cascade-Sierra Nevada axis into northern Baja California (var. *murrayana*), and has an outer Coast Range occurrence from coastal northern California into Alaska (var. *contorta*).

Pinus alvordensis Axelrod, Carnegie Inst. Wash. Publ. 553: 251, pl. 42, fig. 4, 1944. TYPE: U.S.A. Oregon: Alvord Creek. U.C. Mus. Pal., holotype 2095. Figures 77–84.

Supplementary description. Cone ovate, markedly asymmetrical and reflexed, rounded proximally, with a blunt apex; 3 cm long and 2 cm broad; peduncle short and thick, about 4 mm broad, 3 mm long (broken); 6 rows of cone scales, with sharply triangular, attenuated apophyses, slightly curved. Needles in 2s, 2.7–3.0 cm long, 1 mm broad, acute tips, base with a rounded sheath, 2–3 mm long, 2.0–2.5 mm broad. Winged seeds 1.5–2.0 cm long, 0.4–0.6 mm broad, wings slender, markedly acute distally; seed ovate, 5–6 mm long, acute distally.

Discussion. The cone from the Bull Run flora, northern Nevada, falls readily within the Subsect. *Contortae.* The relatively small size of the cone suggests that it may represent an early member of the group, although in the light of only a single specimen this cannot be demonstrated. The age of the deposit at this site (Loc. P 572–5) is 38 Ma, or Late Eocene. The associated flora represents a pure montane conifer forest of *Abies* (3 spp.), *Picea* (3 spp.), *Pinus* (2 spp.), *Larix, Tsuga,* and *Chamaecyparis* as dominants, with rare small leaves of forest shrubs, notably species of *Crataegus, Mahonia, Prunus,* and *Vaccinium.*

Slender winged seeds in the Creede flora, Colorado, are sufficiently similar to the Alvord Creek specimen to be referred to it. The Creede specimens are from 1.5 to 2.0 cm long, wings narrowly elongate, acute to rounded distally, wing 4–5 mm broad, seed proper about one fourth size of wing; tip acute; seed permanently attached to wing.

The needles in 2s are broadly similar to those of *P. sanjuanensis* Axelrod from the Creede flora. The latter can be distinguished because the fascicle sheath is smaller as compared with those of *P. alvordensis.*

There is no clear evidence that fossils from these sites are allied to any one of the modern varieties of *P. contorta,* although this may be modified as larger collections become available.

Occurrence. Creede, Colorado: U. Colo. Mus., hypotypes 19706, 19707; hypotype 19709; U.C. Mus. Pal., hypotypes 7174–7175, 7237,

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FIGURE 73. *Pinus truckeensis* Axelrod, sp. nov. Celetom Quarry, 30 km E. of Reno, Nevada. U.C. Mus. Pal., paratype 2224. Late Miocene, 13 Ma.

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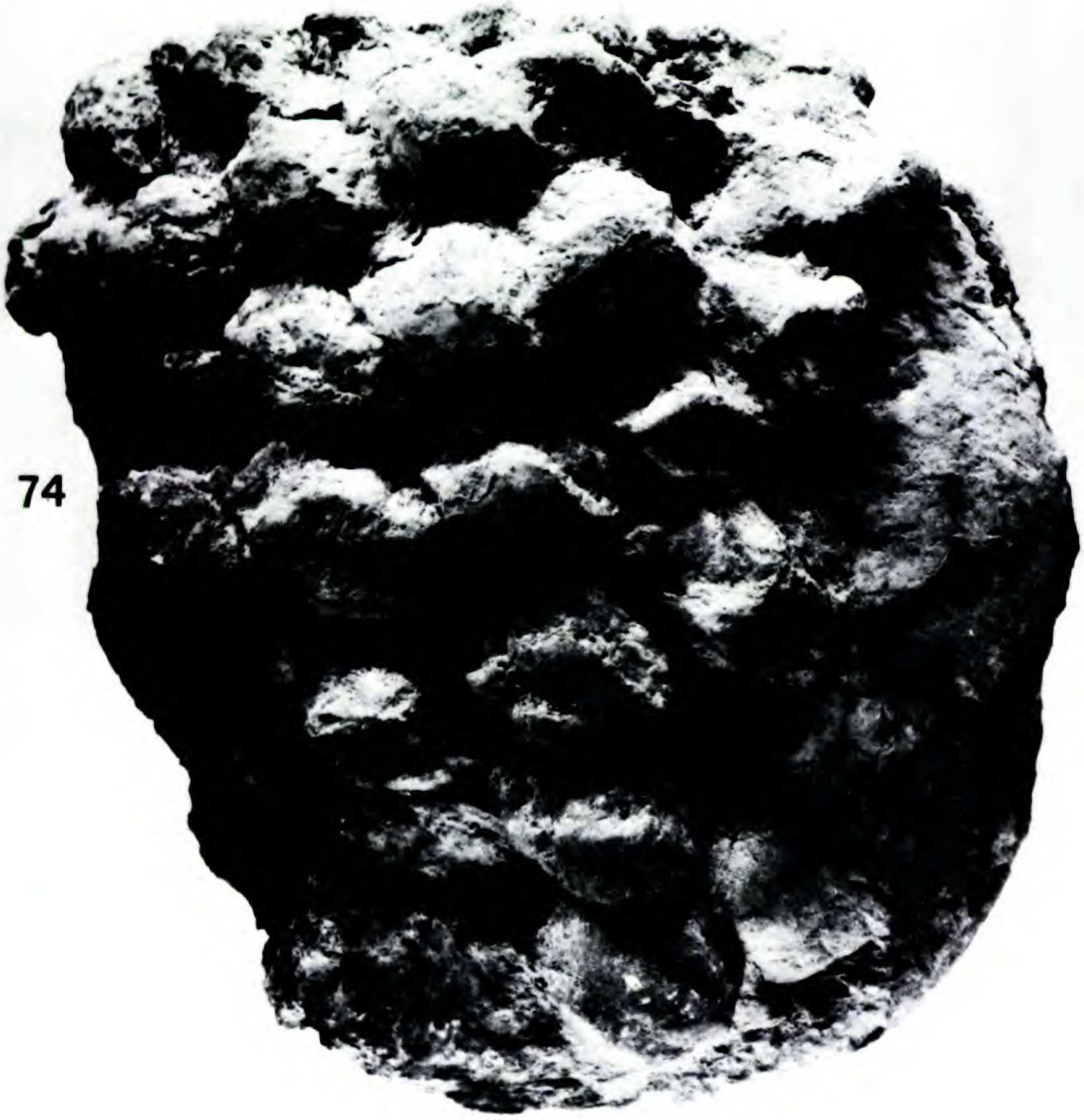

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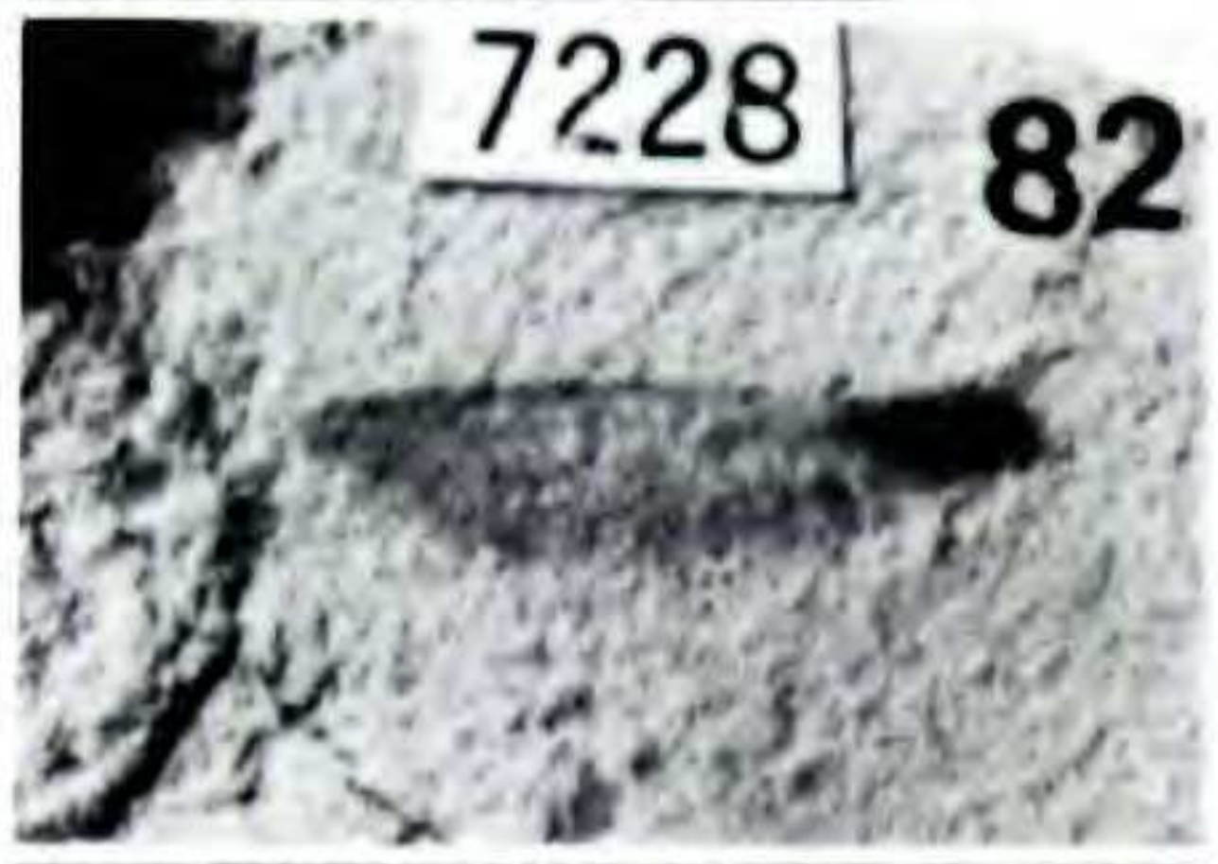

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homeotypes 7228–7230, 7235–7238, 7176, 7245; Bull Run, Nevada: U.C. Mus. Pal., hypotypes 7231–7232.

Subsect. *Oocarpae*

This alliance now occurs in California, southwest Oregon, and in Mexico. The California taxa, *P. muricata* D. Don, *P. radiata* D. Don, and *P. remorata* Mason form discontinuous populations along the central and southern California coast, whereas *P. attenuata* Lemmon has a scattered distribution in the interior. Those in Mexico, *P. greggii* Engelm., *P. oocarpa* Schiede, *P. patula* Schiede, and *P. pringlei* Shaw, are in the Sierra Madre Occidental and Oriental, and with *P. oocarpa* ranging south into Nicaragua (see maps in Critchfield and Little, 1966).

Pinus burtii Miller, Torrey Bot. Club Bull. 105: 93–97, figs. 1–9, 1978. TYPE: U.S.A. Massachusetts: Martha's Vineyard. U.S. Nat. Mus., holotype 222868. Figure 85.

This large cone comes from a Miocene greensand associated with vertebrate and invertebrate fossils at the north end of cliffs at Gay Head, Martha's Vineyard, Massachusetts (Miller, 1978). The mammals are of Early Miocene (Late Arikareean) age, or about 22 Ma according to D. Savage (pers. comm., 1984).

Based on its external and internal structure, Miller considered the cone a member of the *Oocarpae*. It differs from living species of the group in its long, cylindrical outline and large swollen apophyses. It differs from cones of the *P. radiata* populations in California, which are largely asymmetrical; *P. oocarpa* has smaller, more nearly ovate cones; *P. attenuata* has strongly hooked apophyses and is asymmetrical; and the Mexican species *P. patula, P. greggii,* and *P. pringleii* are more slender and tend to be asymmetrical, and the apophyses are subdued.

There may be a relationship between *P. burtii* and *P. O'Donnellii* Teixeira from the Miocene of Lisbon (see Gaussen, 1960, fig. 365: 1). If so, this would be another Miocene trans-Atlantic link.

The occurrence of a member of *Oocarpae* in the eastern United States provides an additional link with the upland flora of the Sierra Madre Oriental, a distribution discussed by others (Harshberger, 1911; Axelrod, 1960: 267–269; Graham, 1973; Greller & Rachele, 1983).

Pinus celetomensis Axelrod, sp. nov. TYPE: U.S.A. Nevada: Celetom Quarry 25 km east of Reno. U.C. Mus. Pal., holotype 7233. Figure 86.

Cone large, elliptic-ovate in outline, fully 14–15 cm long, 7.5 cm broad; base obtuse, tip acute; 10 and 13 rows of scales, those in middle 1.5–1.7 cm broad and 8–9 mm high, swollen, broadly rounded, asymmetrical and upcurved; apophyses strongly reflexed proximally and flattened on outer (anterior) side, less so distally; umbo centro-mucronate, the mucro very small, scarcely 1 mm long.

Discussion. This appears to be a new species of Subsect. *Oocarpae.* The cone is of the average size of the Año Nuevo population of *P. radiata.* It differs from *P. radiata* cones of this size in that the fossil is elliptic-ovate, not ovate, the apophyses are swollen to the distal end of the cone rather than being confined chiefly to its upper third or half. In addition, the apophyses are more flattened throughout and are reflexed proximally in the fossil; in *P. radiata* the apophyses are more evenly rounded and hence unlike the fossil.

This cone seems intermediate between those produced by *P. radiata* and *P. attenuata.* It differs from cones of *P. attenuata* in that the apophyses are not sharply acute or hooked. Whether the present specimen represents a form transitional between *P. radiata* and *P. attenuata* can only be determined when additional fossil specimens become available.

Pinus celetomensis was adapted to an interior, subhumid climate as judged from the composition of the nearby Purple Mountain flora which

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FIGURES 74–84.—74. *Pinus pieperi* Dorf. Mount Eden, California. U.C. Mus. Pal., hypotype 7227. Latest Miocene, 5–6 Ma. Water-worm cone.—75, 76. *Pinus hazeni* Axelrod. Mount Eden, California. U.C. Mus. Pal., hypotypes 7225, 7226. Latest Miocene, 5–6 Ma.—77, 78. *Pinus alvordensis* Axelrod. Bull Run, Nevada. U.C. Mus. Pal., hypotypes 7232, 7231. Late Eocene, 40 Ma.—79–82. *Pinus alvordensis* Axelrod. Creede, Colorado. U.C. Mus. Pal., hypotypes 7174, 7175, 7173, 7228. Latest Oligocene, 26.5 Ma.—83, 84. *Pinus alvordensis* Axelrod. Creede, Colorado. U. Colo. Mus., hypotypes 19706, 19707. Latest Oligocene, 26.5 Ma.


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represents vegetation in the ecotone between broadleaved sclerophyll forest and mixed conifer forest (Axelrod, 1976).

Pinus diegensis Axelrod & DeMéré. San Diego Soc. Nat. Hist. Trans. 20(15): 291, figs. 6A–B, 7A–B, 1984. TYPE: U.S.A. California: San Diego Formation. Holotype SDSNH 25135, paratypes 25110, 25136, 25137.

This recently-described pine of the *P. radiata* alliance is from Chula Vista, near San Diego, California. The species produced cones much like the present population *P. binata* on Guadalupe Island. The cones show considerable variation in size, symmetry, and apophyses development, as noted earlier by Howell (1941). The occurrence of such a pine on the mainland suggests that the insular species did not originate in isolation, and that it may have been ancestral to the present California populations at Monterey, Año Nuevo, and Cambria.

Pinus lawsoniana Axelrod, *in* R. N. Philbrick (ed.), Sympos. Biology of California Islands, p. 115, pl. 1, figs. 1, 2, 1967. TYPE: U.S.A. California: Old Forest Soil on Mussell Rock. U.C. Mus. Pal., holotype 20533, paratype 20534. Figures 90, 91.

Pinus masonii Dorf., Carnegie Inst. Wash. Publ. 412: 70, pl. 5, fig. 6 only, 1930.
Pinus pretuberculata Axelrod, Carnegie Inst. Wash. Publ. 476: 166, pl. 3, fig. 3 only, 1937.

Cones similar to those of *Pinus radiata* D. Don occur in rocks about 5–6 Ma old at Mussel Rock, on the outer coast south of San Francisco. They were recovered there by A. C. Lawson in 1893 from an old forest soil that rests on Jurassic diabase and *underlies* the marine Merced Formation. Similar cones are in the Mount Eden flora (Axelrod, 1937, pl. 3, fig. 3) dated at 5–6 Ma, and the Lower Pico Formation about 3 Ma old (Dorf, 1930, pl. 5, fig. 6).

Cones in the Chula Vista Formation south of San Diego are allied but were named *P. diegensis* Axelrod & DeMéré (1984) because they exhibit variation most like cones produced by the Guadalupe Island population. The specimens from Mussel Rock and Mount Eden seem more similar to those of the present Monterey population.

Occurrence. Mt. Eden, California: Mus. Nat. Hist. Los Angeles, hypotype L-1306;1014/688; Pico, California: U.C. Mus. Pal., hypotype 307.

Pinus pretuberculata Axelrod, Carnegie Inst. Wash. Publ. 476: 166, pl. 3, fig. 4 only, 1937. TYPE: U.S.A. California: Mount Eden. Nat. Hist. Mus., Los Angeles Co., lectotype 1014/696. Figures 87, 89.

Pinus pretuberculata Axelrod. Condit, Carnegie Inst. Wash. Publ. 553: 74, pl. 14, fig. 1, 1944; Axelrod, Univ. Calif. Publ. Geol. Sci. 34: 127, pl. 18, figs. 3–4, 11–13, 1958.

Discussion. Cones of this species have been recorded from the Mount Eden flora, southern California (Axelrod, 1937), the Table Mountain flora from the central Sierran foothills (Condit, 1944), and the Verdi flora of western Nevada (Axelrod, 1958). The Table Mountain flora is well dated at 12 Ma, the Mount Eden and Verdi are 5–6 Ma old. These records illustrate that the species had a wider distribution than its modern derivative, *P. attenuata* Lemmon, consistent with its new record at Celetom Quarry, Nevada.

The Celetom record, from diatomite in the lower part of the Coal Valley Formation, consists of the upper half of a cone estimated to have been 12 cm long and 6 cm broad at its widest part. There are 9 × 6 rows of scales preserved, the apophyses are conical, swollen, upswept to reflexed, and excentro-mucronate. The inside face (posterior) of the cone is missing, but there is evidence of smaller cone scales on the outer left margin so that it is apparent that the cone is asymmetrical. The cone scales are marked by prominent ridges on the outer sides so that in cross-section they are generally rhombic.

This cone appears to be typical of populations in the Sierra Nevada to the west, and especially

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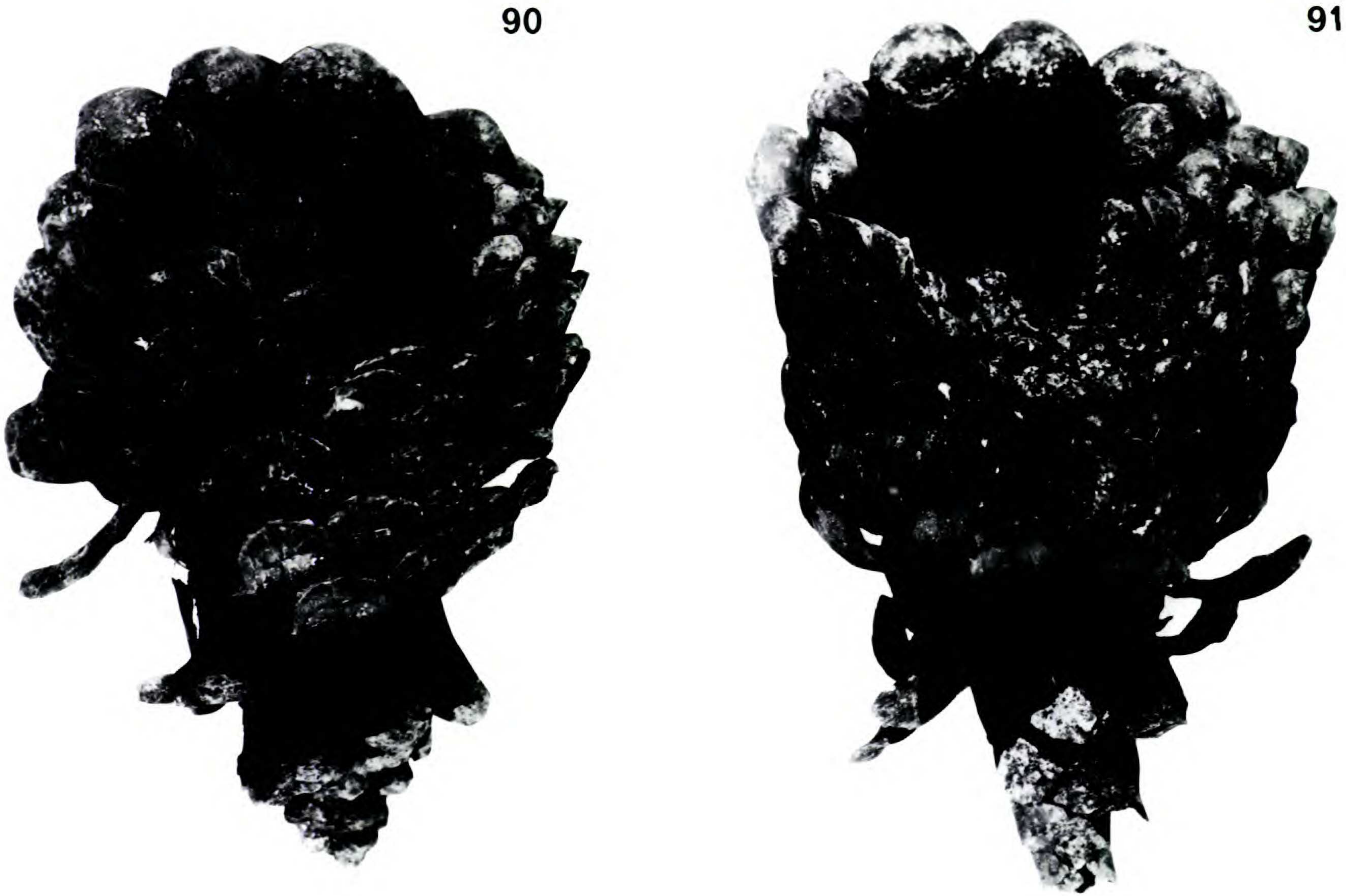
FIGURES 85–89.—85. *Pinus burtii* Miller. Martha's Vineyard, Mass. U.S. Nat. Mus., holotype 222868. Early Miocene, ca. 22 Ma. (From Miller, 1978.)—86. *Pinus celetomensis* Axelrod, sp. nov. Celetom Quarry, 30 km E. of Reno, Nevada. U.C. Mus. Pal., holotype 7233. Late Miocene, 12 Ma.—87. *Pinus pretuberculata* Axelrod. Celetom Quarry, 30 km E. of Reno, Nevada. U.C. Mus. Pal., hypotype 7234. Late Miocene, 12 Ma.—88. *Pinus tiptoniana* Chaney & Axelrod. Tipton, Oregon. U.C. Mus. Pal., lectotype 129. Middle Miocene, 15 Ma. (Previously figured by Chaney & Axelrod, 1959.)—89. *Pinus pretuberculata* Axelrod. Table Mountain, California. U.C. Mus. Pal., hypotype 2720. Late Miocene, 12 Ma. (From Condit, 1944.)



FIGURES 90, 91.—90. *Pinus lawsoniana* Axelrod. Mussel Rock, S. of San Francisco, in forest soil below basal Merced Formation. U.C. Mus. Pal., holotype 20533. Late Miocene, ca. 5–6 Ma. (From Axelrod, 1967a.)—91. *Pinus lawsoniana* Axelrod. Mussel Rock, S. of San Francisco, in forest soil below basal Merced Formation. U.C. Mus. Pal., paratype 20534. Late Miocene, ca. 5–6 Ma. (From Axelrod, 1967a.)

to those in southern California that have more prominent apophyses. The modern *P. attenuata* occurs in the lower part of the forest belt, often forming nearly pure stands where it has been disturbed by fire. The species ranges discontinuously from southwestern Oregon into northern Baja California. In the south, it is regularly adjacent to the upper chaparral belt at the forest margin.

Occurrence. Table Mt.: U.C. Mus. Pal., hypotype 2720; Verdi, Nevada: MUC. Mus. Pal., hypotypes 1972–1975, homeotype 1971; Celetom Quarry, Nevada: U.C. Mus. Pal., hypotype 7234.

Pinus masonii Dorf, Carnegie Inst. Wash. Publ. 412: 70, pl. 5, figs. 4, 5 (not fig. 6 which is *P. lawsoniana* Axelrod), 1930. TYPE: U.S.A. California: Merced. U.C. Mus. Pal., holotype 308, paratype 306. Figure 94.

Pinus masonii Dorf. Axelrod, *in* R. N. Philbrick (ed.), Sympos. Biology of California Islands, p. 117, pl. 5, figs. 1–2, 4–5; pl. 6, fig. 2, 1967. Axelrod, Univ. Calif. Publ. Geol. Sci. 120: 39, pl. 12, figs. 1–4, 1980.

This pine, rather rare in pre-Pleistocene coastal deposits of California, has cones similar to those of *P. muricata* D. Don., now distributed discontinuously from the north coast of California southward into northern Baja California near Eréndira. Over this broad area the scattered populations are represented by three varieties (Axelrod, 1983a).

Its known fossil records are in the Lower and Upper Merced Formations on the coast south of San Francisco (Dorf, 1930; Axelrod, 1967, 1980), in the upper part of the Lower Pico Formation on the coast west of Ventura (Dorf, 1930), and in the Upper Pico Formation north of Santa Paula (Axelrod, 1967). The oldest of these records in the basal Merced Formation, is about 5 Ma.

Occurrence. Lower Pico, California: hypotypes 12738, 20380; Upper Pico, California: hypotype 20380.

Pinus tiptoniana Chaney & Axelrod, Carnegie Inst. Wash. Publ. 617: 142, pl. 13, figs. 3–6, 1959. TYPE: U.S.A. Oregon: Blue Mts. U.C. Mus. Pal., lectotype 129, paratypes 128, 643, 2866, 2867, 2869, homeotypes 642–644, 2868, 2870–2871. Figure 88.

This pine from the Blue Mountains flora, eastern Oregon, occurs in diatomaceous sediments interbedded with basalts of the Columbia River Lava Group. The fossil was compared initially with *Pinus halepensis* Miller, which it does resemble. However, comparison with cones in the collection at the Institute of Forest Genetics, Placerville, shows that *P. tiptoniana* is a member of the *Oocarpae.* This is indicated by the umbo, which is centro-mucronate, whereas in *P. halepensis* it is excentro-mucronate. *Pinus tiptoniana* appears to be an extinct species of the group, differing from those most nearly allied to it, e.g., *P. patula* Scheide & Deppe and *P. pringlei* Shaw, in having needles in 2s, and the fossil cones appear to be more nearly symmetrical as judged from the incomplete specimens. These modern pines allied to *P. tiptoniana* occur in the Sierra Madre Oriental, Mexico, generally at middle elevations in woodlands and forests adapted to a climate of high equability and ample summer rain.

PLEISTOCENE *OOCARPAE* FROM COASTAL CALIFORNIA

The following is a listing of younger records of *Oocarpae* from coastal California. Some of these deposits (e.g., Carpinteria, Pt. Sal) are (were) especially rich in cones that accumulated on floodplains. This is because the cones were not dispersed as widely by currents as in the case of the rare cone records from most marine deposits.

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FIGURES 92–94.—92. *Pinus radiata* D. Don. Santa Barbara Formation, Veronica Springs Quarry, Santa Barbara, Calif. Santa Barbara Mus. Nat. Hist., hypotype 473. Early Pleistocene, ca. 1 Ma. A cluster of four cones. (Previously figured by Axelrod, 1980.)—93. *Pinus muricata* D. Don. Upper Merced Formation, S. of San Francisco. U.C. Mus. Pal., hypotype 159. Early Pleistocene, ca. 1 Ma. (Previously figured by Mason, 1932 and Dorf, 1930.)—94. *Pinus masonii* Dorf. Lower Merced Formation, S. of San Francisco, Calif. U.C. Mus. Pal., hypotype 20532. Pliocene, ca. 3. Ma. (Previously figured by Axelrod, 1967.)

FIGURES 95–103. *Pinus muricata* D. Don, var. *borealis* Axelrod. Near Point Sal, Santa Barbara Co., Calif. U.C. Mus. Pal., hypotypes 20400–20408. Late Pleistocene, ca. 26,700 ± 800 years B.P. (From Axelrod, 1967.)

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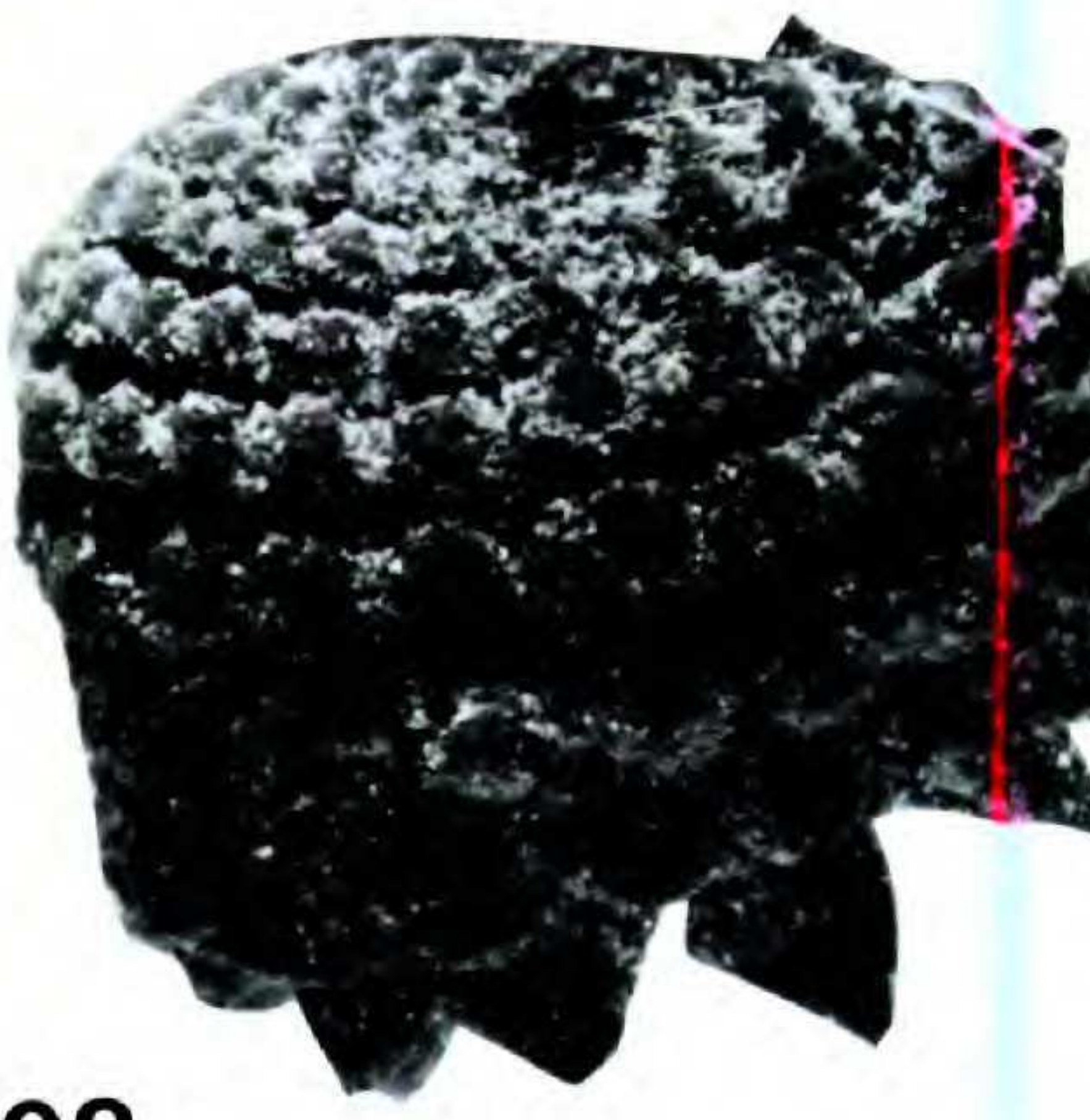

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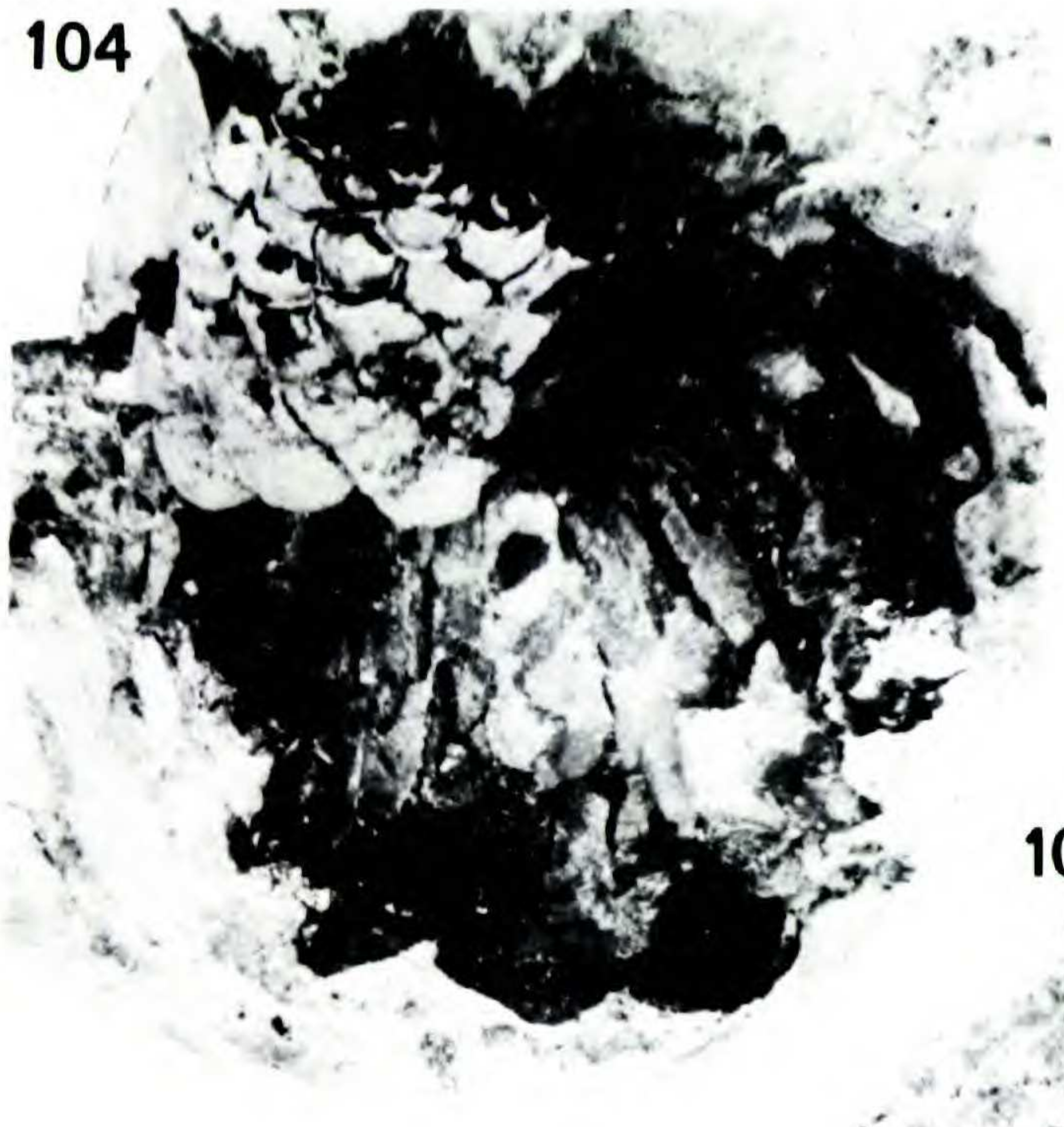

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FIGURES 104–108.—104, 105. *Pinus remorata* Mason. Century City, Los Angeles. U.C. Mus. Pal., hypotypes 5841, 5840. Plio-Pleistocene transition, ca. 2 Ma.—106. *Pinus remorata* Mason. Santa Cruz Island, Willow Creek. U.C. Mus. Pal., hypotype 5839. Late Pleistocene, 14,200 ± 250 years B.P.—107. *Pinus remorata* Mason. Near Point Sal, Santa Barbara Co., Calif. U.C. Mus. Pal., hypotype 5840. Late Pleistocene, 26,700 ± 800 years B.P.—108. *Pinus remorata* Mason. Carpinteria, Calif. Santa Barbara Mus. Nat. Hist., hypotype 474. Late Pleistocene, older than 38,000 years B.P. (All specimens previously figured by Axelrod, 1980.)

Pinus attenuata Lemmon.
  Late Pleistocene
    Oakland (Metcalf, 1923).
  Early Pleistocene
    Seacliff (Axelrod, 1983); Signal Hill (Mason, 1932; Axelrod, 1967).

Pinus muricata D. Don. Figures 93, 95–103.
  Late Pleistocene
    var. *muricata*. Rancho La Brea (Mason, 1927).
    var. *borealis*. Millerton (Mason, 1934); Carpinteria (Chaney & Mason, 1933; Axelrod, 1967, 1980).
  Early Pleistocene
    var. *muricata*. Seacliff (Axelrod, 1983); Wilmington (Axelrod, 1967).
    var. *stantonii*. Seacliff (Axelrod, 1983).

Pinus radiata D. Don. Figure 92.
  Late Pleistocene
    Millerton (Mason, 1934); Drakes Bay (Axelrod, 1980, 1983); Thornton Beach (Axelrod, 1967); Pt. Sal (Axelrod, 1967); Carpinteria (Chaney & Mason, 1933); Santa Rosa I. (Axelrod, 1980); Rancho La Brea (Mason, 1927; Warter, 1976); Little Sur (Langenheim & Durham, 1963).
  Early Pleistocene
    Potrero Canyon (Axelrod, 1967); Seacliff (Axelrod, 1983); Century City (Axelrod, 1980); Spring Valley Lake (Axelrod, 1967); Veronica Springs (Axelrod, 1980).

Pinus remorata Mason. Figures 104–108.
  Late Pleistocene
    Carpinteria (Chaney & Mason, 1933; Axelrod, 1980); Santa Cruz I. (Chaney & Mason, 1930); Pt. Sal (Axelrod, 1967).
  Early Pleistocene
    Potrero Canyon (Axelrod, 1967); Century City (Axelrod, 1980), Seacliff (Axelrod, 1983).

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